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ON THE PHYSIOLOGY OF REPRODUCTION IN PLANTS.¹

BEHIND every morphological phenomenon there stands a physiological question. Problems which can be tentatively dealt with in two ways, according to the relative importance assigned to the morphology and the physiology of the organism are still continually arising in Botany, as they have arisen—in various guises—in the past, and it would probably be not difficult to classify most of the combatants in the great disputes of the science into two groups, the one including those who are especially prone to judge biological causes on physiological evidence, the other those who regard morphological data as of primary importance.

The point of view has exerted considerable influence in the study of plants, whether we turn our attention to textbooks or to the monographs of the investigator, and the warnings prompted by the clear-sighted vision of a few strong observers, of the dangers of allowing Botany—the study of plants—to be torn into shreds of narrow specialisation, superficial generalisations, and mere vapourings of transcendentalism, are justified by the departures of the last twenty years.

¹ Die Bedingungen d. Fortpflanzung bei einigen Algen u. Pilzen. Von Professor Dr. G. Klebs. Jena, Gustav Fischer, 1896.

Beiträge zur Lehre von der Fortpflanzung der Gewächse, von Professor Dr. M. Möbius. Jena, Gustav Fischer, 1897.

In no branch of the subject have these dangers been more apparent than in the study of the Thallophytes ; though, possibly, examples are oftener quoted from among the Flowering Plants, because the facts seem easier to obtain and more obvious.

The morphological doctrine known as the alternation of generations is a case in point with reference to the former ; while the disputes as to the relation of highly adapted—specialised—plants, such as *Xerophytes*, to their environment afford examples in the latter connection.

It being admitted that the alternation of generations as matter of fact exists in the *Bryophyta* and *Pteridophyta*, the attempt to read the dogma into the life history of the Thallophytes has been made so often and so persistently that the unwary or insufficiently informed are liable to suppose it is more successful than is really the case, while even more cautious speculators seem to be persuaded it is necessary—a consequence of persistence as it were.

Again it occurs, largely owing to misapprehensions of the real difficulties which Darwin saw so clearly, that some botanists regard the case for a *Xerophyte*—as a particular example—being structurally the direct outcome of the persistent actions of the environment, as much more nearly capable of demonstration than the present condition of science allows.

Morphologists divide the life-cycle of a Moss into two parts. The Moss-plant (*Gametophyte*), arising as a vegetative outgrowth from the protonema of the germinating spore, ending in the production of the oosphere, etc., being the one ; the Sporogonium (*Sporophyte*) constituting the other.

If we ask why *two* generations? Why the profound structural differences between the protonema and the leafy stem, their sharp segmentation, entire change of growth, cell-division, etc., do not justify our making a third break here in the life-cycle? The morphologist replies because the organic separation between embryo and gametophyte on the one hand, and between protonema and sporophyte on the other, are so complete that in each case a breach of

organic continuity is established which justifies our regarding the two alternate "generations" as we do. It is clear, however, that some assumptions lie behind this, and that tacit necessity for fitting in the life-history to the ascertained alternation in Ferns plays some part; for, in the first place, mere breach of continuity would apply to any naturally separated tubercule or bud or even a piece of protonema, and, in the second, we know that the protonema need not arise from a spore, but may be developed from any part of the gametophyte or sporophyte—*e.g.*, a rhizoid, a piece of stem, or of seta, etc.

Obviously one underlying assumption is that the normal life-history does not admit of the breaches of vegetative continuity, or of the "misplaced" origins of protonema referred to above.

But *normal* means *usual* in these cases. The same applies to the Ferns, where apospory and apogamy have now, moreover, been shown to be so common that one is almost driven to ask how soon it will be necessary to take a sort of census as to the proportion of cases where "normal" alternations of generations occur, and those where we find the new Fern-plant—the *Sporophyte*—springing direct from the previous sporophyte without the intervention of the gametophyte-generation; or sporangia springing direct from the prothallus, and so on.

The absolute number of these "abnormal" cases is at any rate large, and when we come to look over the whole domain of the Cryptogams, our doubts as to any fixed *necessity* for the alternation of generations increase in proportion as the question, How far is it all a matter of conditions of nutrition, moisture, illumination, temperature, etc.? assumes definite shape. For however much we may assent to the typical character of alternations of generation in *Bryophyta* and *Pteridophyta*, we must concede that such alternation is not essential, and the gradual reduction of one generation in the higher plants till it is merely represented by the most obscure traces, detected only with difficulty and by special methods, is a further proof of this.

Returning to the second of the classes of cases selected above—How far may we conclude that the peculiar organisation of such specialised plants as Xerophytes, for instance, are due to the continued action of their present environment, and how far to the accumulated inherited effects of the environment in the past? For that is what the dispute between the two great schools amounts to. In other words, how far will the plant continue to build up its structures and assert its morphological individuality, independently of variations in the environment, in virtue of the machinery it possesses being compelled to work along definite lines if the environment allow it to work at all; or how far can the action of the existing environment affect the working of that machinery in the present, and bring about variations which we can detect?

It is clear that experiment alone can give us information here; but the results of the experiments already made go to show that we have still much to learn before we can even realise the nature in detail of the problem to be attacked.

Are we, when experimenting with a varied environment, directing its actions on to a complex of structures which are themselves the response to the continued action of this environment; or are other factors in play—*e.g.* the accumulated and emphasised results of previous environments handed down by heredity?

Most botanists would probably say the latter, and indeed it seems difficult to see how the former could be maintained, although some such assumption would appear to lie at the foundation of some of the experimental enquiries started or proposed.

It seems evident that a clear apprehension of this question must precede any enquiry into the action of the environment on plants, but that once obtained we need not be deterred even by the enormous complexity of the subject from admitting that all the phenomena of morphology, including the alternation of generations, are phenomena with physiological questions behind them, and therefore subjects for experimental enquiry.

Glimpses are already to hand which show that such is

the case. Some Liliaceous plants never produce seeds, unless experimentally forced to do so, because the stores of food-materials are all deflected into the bulbs—the rudimentary gametophyte is starved and dies of inanition, and yet we have no reason to believe that the ever-continued sporophyte suffers. Species of *Musa* and many other plants have probably never formed seeds for thousands of years, and in such cases as these and the potato and many other flowering plants, where the sporophyte is propagated vegetatively, we have no reason to believe that the plant suffers, though in many of them no trace of the gametophyte generation ever appears at all.

It looks then as if the environment may have more to do directly with the origin of reproductive organs—and with that of other structures also, be it said—than is often assumed.

In these classes of cases it is soon evident that matters are too complex for direct experimental treatment, at least just now, and we may feel very sure that all hope of solving fundamental questions concerning the relations between the morphology and physiology of sexual organs must be approached through the lower and simpler forms of life. Striking illustrations of variation, or of morphological inconsistency, are doubtless more easily obtained from higher plants than from lower, and probably because the very complexity of their organisation renders them more easily varied—deflected out of the normal course—on a similar principle to that which renders a tall house of cards more easily overthrown by a shock than a less ambitious erection would be; but when it comes to studying the factors at work which induce the variations it is perhaps logical to expect that the study of the lower plants will be more productive of results. But we must not forget that a very slight variation in a lower plant may imply more than a much more obvious change in a higher one.

In this connection the recent publication of Kleb's experiments on the conditions affecting the development of reproductive organs in some Algæ and Fungi is one of the most valuable and stirring contributions to botany of this decade.

Klebs' book *Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen* will have a peculiar value to all botanists interested in Cryptogams and especially in Thalophytes, and this in three connections. First, it is a record of very numerous and careful observations of the conditions affecting the life of several types of fresh-water Algæ, and of experiments pushed so far that it seems now possible to be sure of growing these particular forms at will in the laboratory by insisting on the maintenance of the conditions. That this will be a boon to those who have hitherto depended on accidental supplies of Algæ from outside, hurriedly collected and brought the day before into an environment which may be detrimental or not to these delicate organisms, is obvious; but it will also afford much help to those who have had sufficient experience to know what Algæ they can and what they cannot grow in the laboratory, and must lead to extensions of power in this connection.

Secondly, Klebs gives very clear directions for the separation and pure culture of minute and intermixed fresh-water Algæ on solid media and in liquids, and it should be a stimulus to many new departures when it is known that these organisms can be treated in similar ways to Fungi and Bacteria in this respect. True, we have known for some time that something may be done towards isolating pure cultures of Algæ, and Beyerinck and others have given clear indications of success, but Klebs carries this subject further than ever before, and shows how we may look for rules of isolation and pure cultures of Algæ as trustworthy as those for other organisms. The application of all this is obvious, but Klebs points the moral by himself showing that even observers so astute and able as Woronin and Rostafinski confounded two organisms in their celebrated study of *Botrydium*, and puts this so convincingly that Strasburger has accepted and already reproduced the result in his recent edition of the *Botanische Practicum*, just published. The criticism of those startling observations which Chodat,¹ Borzi and others have recently

¹ Chodat has replied to Klebs in a recent number of the *Arch. des Sc. Phys. et Nat de Geneve*, t. iii., Jany. 1897.

offered on the polymorphism of the lower green Algæ, stands so firmly on the new foundations which Klebs gives it, that one is constrained to believe much of this work must be re-examined by the help of the strict methods enjoined by him.

Thirdly, the especial object of the work is to show that, having learnt to isolate and grow a green Alga, its behaviour will vary according to the conditions of the environment. This of course would be generally conceded, but the point is that the exact conditions which induce or govern a given biological reaction can be discovered and controlled, and so our knowledge is altered from an indefinite conviction that you must not do this, that, or the other, to an Alga, or it will not grow, or multiply, or succeed generally, to the definite surety that if you want a given Alga to produce zoospores you must treat it in such and such a manner, and if you alter the treatment according to directions you can make the Alga form sexual organs, and so on.

It sounds almost absurdly impossible when put in such a form, and yet many of Klebs' experiments show that his fifteen years or so of study of these reactions have resulted in knowledge so clear and so definite of the exact conditions necessary to induce a given biological response, that one may almost compare the operations with those of a chemist who calls forth a predicted change in a substance in a test tube by adding another substance to it.

When we are told that *Conferva*, for instance, after being cultivated for twenty-two days in a 1 per cent. galactose solution, in which it forms no zoospores, at once proceeds to form them if transferred to a solution of aesculin, and that the whole experiment is carried on in the dark, our ideas begin to receive shocks which lead us on from total revolt to wondering acquiescence and conviction in proportion to our acquaintance with the number of recorded experiments, the care and fulness of the records, and the character of the evidence generally.

But the work teems with equally startling results, of which I shall have space to quote a few instances only.

Vancheria repens, if growing on solid media in damp

air in the light, can be kept for months and years without forming zoospores; yet at any time zoospores can be obtained by plunging it into water.

The alga can be cultivated easily in the well-known Knops' nutritive fluid of inorganic salts, and in 0.2-0.5 per cent. solutions grows well but forms no zoospores so long as the salts are supplied; yet at any time vigorous plants removed to pure water at once develop zoospores.

Cultures in water only, or in very dilute salt solutions—0.1-0.2 per cent.—in the light, remain sterile: but darkening them more or less completely at once induces zoospore formation.

If exclusion of light is combined with either of the two foregoing methods the stimulus to zoospore-formation is quickened.¹

In these cases the first zoospores appear in less than twenty-four hours, and go on forming for weeks. A most interesting discussion follows as to the nature of the changes.

This is supplemented by experiments on the effects of temperature, various light-rays, osmosis, organic nutritive materials, mechanical stimuli, etc, and even if the reader does not accept all Klebs' few and cautious conclusions as to the probable actions of the various factors, he can scarcely escape two convictions, *viz.*: (1) that in such an Alga, every factor of the environment produces its own effect as it varies, and (2) Klebs has shown that strict experimental methods can be applied to the solution of the problem as to what that effect results from.

It is premature to generalise widely from the results of this work, since Klebs promises us another book containing his conclusions, this first instalment being confined almost entirely to the detailed descriptions of the experiments. Nevertheless one cannot avoid drawing comparisons between the effects of light, temperature, moisture, food-materials, etc., in stimulating the production of asexual or sexual organs in these Thallophytes, and the effects of the same agents in forcing higher plants to propagate by

¹ The general truth of this has been confirmed by Miss Pertz in the laboratory in Cambridge.

asexual organs or to flower. The results are not always the same, however, in either case. At the outset, some species respond to a given stimulus fairly readily: others again show little or no response, and it seems as if much yet remains to be done ere we can explain the specific differences.

One is struck with the apparent similarity between the cases where *Vaucheria* remains sterile in moving water, as Klebs finds, and those of many flowering aquatics which are also sterile in quick streams. Schenck,¹ for example, says species of *Hippuris*, *Sagittaria*, *Alisma*, *Juncus*, *Littorella*, *Elatine*, *Sparganium*, *Callitriche*, *Potamogeton*, etc., remain sterile in moving water; and Klebs found that, like *Vaucheria*, *Ulothrix* and *Cedogonium* are both induced to develop zoospores by removal from moving water—which inhibits the process—to still water. Even slowly running water inhibits the formation of sexual organs in *Cedogonium*, and Klebs quotes an experiment (p. 279) where a culture which remained sterile from the 10th of June to the 20th of July in the moving water of his aquarium, at once developed the sexual organs when removed to quiet water. As to *Vaucheria*, he declares that species which remain sterile for months in running water at once form the sexual organs if transferred to still water. The discussion as to possible factors of explanation is very interesting, but too long to reproduce; he cannot explain it in detail. Another interesting point is the experimental proof that transpiration into a relatively dry atmosphere is an essential condition for the development of the conidia of *Eurotium*; and we have convinced ourselves in the Cambridge Laboratory that sexual organs or conidia can be produced by following the directions; and here again one is tempted to draw comparisons with the numerous cases where the on-coming of a dry atmosphere favours the flowering of higher plants, as pointed out by many observers. Moebius,² among others has collected cases showing that dry air and a moist soil

¹ *Biologie der Wassergewächse*, p. 107, 1866. Cited by Möbius, p. 130, *Beiträge zur Lehre von der Fortpflanz.*

² *Beiläuge zur Lehre von der Fortpflanzung.*

will often bring plants to flower which refuse to flower otherwise, or only to a less extent.

Over and over again attempts have been made to correlate the conditions of the environment and the habit of the plants subject to it, some of the most recent being Warming (*Ökologische Pflanzengeographie*, 1896), Gaston Bonnier (*Influence de la Lumière électrique sur la forme, etc.*, Rev. Gen. de Bot, 1895) and Moebius (*Beiträge zur Lehre von der Fortpflanzung*, 1897), but the critical reader always feels that even the most careful experimenter is unable to solve such problems, for two chief reasons: (1) The (higher) plants experimented upon are so exceedingly complex that it is almost impossible to disentangle the reactions to the conditions imposed by the experimenter, from correlated internal changes, and (2) it seems as yet impossible to vary one factor of the environment without at the same time causing others to vary also. For instance, in experiments with higher plants, we cannot modify the intensity or quality of the *light* by means of screens, etc., without at the same time altering the *temperature* of the soil, plant or air: if we vary the *temperature*, then changes in *moisture* are induced, and so on.

Now Klebs has chosen subjects and methods which reduce these difficulties to a minimum. By selecting Algæ, which grow at low temperatures and in water, and by confining his attention to the conditions which affect reproduction, he is able to go nearer to the ideal variation of one factor at a time than most experimenters have done.

The principal Algæ employed are—*Vaucheria*, *Hydrodictyon*, *Botrydium* and *Protosiphon*, *Spirogyra*, *Desmids*, *Edogonium*, *Ulothrix*, *Hormidium*, *Conferva*, *Bumilleria*, *Stigeoclonium*, *Draparnaldia*, *Chlamydomonas*, and *Hydrurus*.

A brief outline of his programme with *Vaucheria* will serve as an index to his choice of conditions. He first investigates the effects of nutrition, moisture, light, temperature, inorganic salts, organic compounds, osmosis, acids and alkalies, the partial pressure of oxygen and the effects of moving water, on the development of the asexual

zoospores; and then he tries their effects on the development of the sexual organs.

Some results have been referred to. The difficulties with light are great, but he comes to the conclusion that apart from the assimilation effects, light-rays have an influence of their own in inhibiting the development of zoospores. Within the wide range of temperature (3° - 26° C) at which *Vaucheria* will grow, the lower temperatures (3° - 8° C) stimulate, while higher ones inhibit zoospore-formation.

Some curious results are obtained with inorganic salts. Plants growing actively in nutritive solutions of suitable strength refuse to form zoospores, and even darkening them—usually a most effective method—will not stimulate to zoospore-formation until the solution is diluted below a certain point. Removal to pure water, however, at once causes them to develop zoospores, and especially if darkened at the same time. It is curious that these effects can be got with solutions of sodium chloride and other salts not usually regarded as nutritive.

Yet this effect cannot be got by transference from sugar solutions to water: though it can if the *Algæ* be transferred from air or water to the sugar solution.

Camphor gave extraordinary results. After eleven days in camphor-water, transference to water caused zoospores to form: on adding camphor again, the process was inhibited, and even darkening failed to bring them—yet after four days in this inhibited state, removal to water induced the formation of zoospores in twenty-four hours, and the *Alga* went on developing them for a week or two: a re-addition of camphor at once stopped it, but removal to water at once stimulated again, and so on.

An interesting discussion follows as to whether the above were osmotic effects, and comparisons of the osmotic equivalents convinced Klebs that the explanation is not to be found here. Nor does the (slight) acidity or alkalinity of the medium explain it, as experiments show.

Oxygen is not necessary, and some surprising results are obtained as to the small quantities of oxygen needed

even for growth; darkened cultures go on producing zoospores for weeks.

I have already referred to the startling results obtained with running and still water.

As regards the sexual organs, affairs are very different. In the first place bright light is necessary for their formation, and secondly, sugar increases the tendency to form them. Cases are quoted where *Vaucheria* was kept growing for four and a half years in salt-solutions absolutely sterile: yet, at any time, removal of a portion to sugar-solutions, and exposure to bright light, induced the formation of sexual organs in four to five days!

It is not a simple question of nutrition, though the sugar is evidently used to afford nutriment; for if fed with sugar in the dark no sexual organs are developed, while they form in the light whether carbon dioxide be excluded or not.

Further experiments convince Klebs there is a light-effect over and above that of assimilation; but that only the inception of the sexual organs depends on light-action, for once incepted they can be made to complete their development in the dark—no new ones forming meanwhile.

The conditions being known, it is easy at any time to obtain pure growths of sterile *Vaucheria*, and with such Klebs found by means of artificial lights the intensity and quality necessary to induce the formation of sexual organs. The experiments with coloured screens are not devoid of ambiguity, but the rays at the violet end of the spectrum seem necessary.

It is impossible to give even a sketch of all the experimental results, and I must conclude with a reference to the marvellous control obtained over the development of the male organs. *Vaucheria repens* normally produces one oogonium and one antheridium side by side at intervals along the filament: by raising the temperature, or by diminishing the air-pressure, Klebs was able to force all the young oogonia to grow out to vegetative branches, or to suppress them altogether, and to increase the antheridia up

to as many as three to seven in a group—in short to convert the hermaphrodite plant into a male one, at the expense of the female organs. It would be interesting to learn how far the spermatozoids are capable of function. The converse conversion could not be made.

No less interesting are the results with other forms. Parthenogenetic spores were produced in *Spirogyra* by plunging the conjugating threads into selected salt-solutions at the critical moment when union of the zygotes was first about to be accomplished; both "male" and "female" cells were thus converted in spores capable of germination. Similar artificial productions of parthenospores in *Ulothrix*, *Chlamydomonas*, etc., were also accomplished.

The inhibition of the zoospores in *Edogonium* by light or by running water—this plant was so wonderfully under control that the author could make it develop zoospores or sexual organs at will by altering the conditions in definite ways—the artificial regulation of the sexes in *Ulothrix*, etc., as well as many other points must be passed over here.

Hydrodictyon affords one of the best examples of all for showing how conditions rule the development of reproductive organs. It practically amounts to this. In any cell of the net, it is possible at any time to cause either asexual zoospores or sexual gametes to be developed by varying the conditions in definite ways. There are perhaps limits to the size of the cells—they must not be smaller than about 0.03 mm. for gametes and 0.2 mm. for zoospores—but at any time during their growth to a length of 10 mm., external conditions will determine whether growth shall continue, or the contents be converted into zoospores or into gametes. Klebs expressly states that he knows no other Alga which is so plastic in these respects, for every vegetative cell is equally capable of forming, at any time, either zoospores or gametes according to the conditions imposed. The importance of these facts with respect to any hypothesis of alternation of generations is obvious.

Enough has been given to show that Klebs' book will have to be reckoned with as one of the best attempts yet

made to bring into the sphere of actual experimental enquiry a subject which has baffled physiologists for a long time.

If we attempt to see what light this throws on the question of alternation of generations the following remarks occur to one :—

Among the Thallophytes we meet with sporogenous tissues giving rise to asexual spores, and with oospores developed sexually, but if we attempt to read into these and their sequence the dogma of alternation of generations, some quaint difficulties arise.

One of the most convincing cases to many minds is that of such Algæ as *Ædogonium*, *Coleochaete*, etc., where if we call the plant or portion which bears the sexual-organs a gametophyte generation, we have to face the difficulty that it may at the same time bear asexual spores. The attempt to get over this by terming asexual spores borne by the gametophyte *gonidia*, and reserving the term *spore* for bodies *indistinguishable from these gonidia by any morphological or physiological character whatsoever* beyond their origin from a so-called sporophyte,¹ carries its own refutation.

Now the principal interest of Klebs' work centres in his proof that asexual zoospores as well as sexual organs can be called forth or suppressed altogether, practically at will, in any part of the life-cycle of even so highly developed an Alga as *Ædogonium*, or of so specialised a Fungus as *Eurotium*, by merely altering the conditions of the environment. To speak of alternate generations in such cases seems impossible: the assumed mark of a generation is here a matter of conditions, simply, and cannot be regarded as a morphological necessity coming into evidence at just such a place and such a time in the life of the plant as is demanded by some special structure and working of the organisation from the beginning.

Few Algæ have been more thoroughly studied than *Ulothrix zonata*; but Klebs shows that it depends on conditions whether a filament forms (1) Zoospores with four

¹ A point already insisted upon by Scott also in his address to Section K, British Association, Liverpool 1896, p. 7.

cilia which at once germinate directly, (2) smaller Micro-zoospores with four or two cilia which also germinates directly, (3) still smaller Gametes with two cilia, which either conjugate and form zygospores, or can be made to act as parthenospores without conjugating, and (4) larger fusiform Zygosporophores with four cilia. Moreover, in the origin of the zoospores, etc., from a cell, it is a matter of conditions (chiefly nutrition and size) whether one, two, four, eight, or even sixteen or thirty-two zoospores are formed in a cell; or whether eight, sixteen or thirty-two micro-zoospores or gametes are formed in one cell, and so on.

One is also struck with the fact that although Klebs resorts to extreme measures in some of his experiments, in the majority of cases the changes of environment are just such as may and do occur in nature.

The following remarks (p. 175) seem worth careful note:—

“Es ist merkwürdig, dass aus der Geschichte der Wissenschaft so wenig gelernt wird. Schon zweimal hat in der Botanik der gleiche Streit über den Polymorphismus geherrscht, zuerst bei den Pilzen und dan bei den Bakterien. Beide male ist dieser Streit aus unfruchtbaren Diskussionen in die richtigen, streng wissenschaftlickten Bahnen geleitet worden, als man die Reinkultur der Organismen als notwendigen Ausgangspunkt für jede Untersuchung in dieser Richtung verlangte.”

While Klebs' book is a model of records of experimental work, full of new points and suggestions, Möbius' “Beiträge zur Lehre von der Fortpflanzung der Gewächse” is rather an interesting *resumé* of facts compiled from various authors who have written on the reproduction of plants. It consists of five chapters; the first an introductory one dealing with the meaning of individual reproduction as related to the maintenance of the species, and the significance of vegetative propagation as opposed to sexual reproduction proper. The point of view is elementary, but a number of interesting facts are collected, and I think he is quite right in insisting on the plant as an individual

and refusing to treat seriously the proposition that all the poplars in France are only parts of an individual. Chapter II. is concerned chiefly with a discussion of the question whether continued vegetative propagation is injurious to the constitution of plants like the Banana, Potato, Poplars, Fruit-trees, and numerous other plants—wild as well as cultivated—which are rarely or never grown from seed. His views are similar to those of a recent American author who has written clearly and suggestively on this subject,¹ and may be shortly put as summing up against the view that varieties or species show signs of deterioration or dying out from this cause.

In the third chapter Möbius discusses the conditions on which the flowering of plants depends. The influence of light, temperature, moisture, and nutrition, etc., are successively examined, but although the facts collected are interesting one feels dissatisfied with the results, partly owing to the cause already mentioned—that experiments in this domain involve such complexities that one is never sure that the response is to a given factor of the environment—and partly because the whole work seems hurriedly written.² Moreover, in this chapter the author gives the only experiments quoted which he has himself performed, and they are distinctly unsatisfactory.

In chapter four, the relations between bud-propagation and reproduction by seeds is discussed, with much reference to Darwin's celebrated chapter in his "Variation of Animals and Plants under Domestication".

By far the most interesting part of the book to most botanists will be the last chapter, in which the author gives a summary of the origin and significance of sexual repro-

¹ T. H. Bailey, *The Survival of the Unlike*, 1896.

² This latter conclusion is borne out by the misprints which are too common (and evidently not all printer's errors) here and elsewhere in the book, e.g., "Do the *Musa* show any signs of deterioration" (a quotation on p. 34), *Bülhen* for *Blühen* (p. 84), *Laryx* for *Larix* (p. 88). Two errors in a quotation on p. 110. *Ranuncutus* (p. 138). *Musa sapientium* instead of *sapientum* repeatedly, and also *Himanthallia* for *Himanthalia* several times.

duction in plants. What is meant by "Die ungeschlechtliche Bildung von Keimen unterbleibt bei den Blütenpflanzen" (p. 162), I do not quite see, unless the author denies that pollen grains are spores, etc. Möbius regards sexual reproduction as advantageous in three ways, (1) Legitimate crossing of individuals helps to fix the characters of the species, (2) Crosses of more remote individuals offer increased opportunities for variations on which natural selection can work, and (3) sexuality gives a means for developing more complex and highly differentiated forms.

H. MARSHALL WARD.

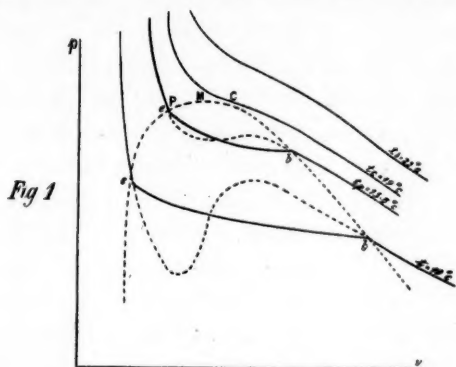
CONDENSATION AND CRITICAL PHENOMENA.

II. MIXTURES OF TWO SUBSTANCES.

THE phenomena which are displayed by mixtures during condensation and near the critical point are more complicated than those of single substances, so much so that a complete explanation of the behaviour of mixtures was not obtained till the phenomena were unravelled by the application of thermodynamics.

Suppose a certain volume of carbonic acid is mixed with a fifth of its volume of air at 0°C . and one atmosphere. Let us define the composition of a mixture as the volume of one of the constituents, here say carbonic acid, in unit volume of the mixture. The composition x of this particular mixture would then be $5/6$. Its properties were investigated by Cailletet and afterwards by the writer of this article. At the temperatures of the experiments, air behaves like a single gas, and the mixture accordingly like a mixture of two substances. When this mixture is compressed at 10°C . the volume diminishes regularly until at a certain moment some liquid is formed. This liquid consists of liquid carbonic acid with some air dissolved in it. As compression goes on the quantity of the liquid increases, but the pressure instead of remaining constant during the process of condensation, as with single substances, goes on rising all the time until the whole of the mixture is in the liquid state. As was shown in the first part of this article even a small quantity of a foreign body is sufficient to bring about an increase of the condensation pressure at diminishing volume. For an actual mixture like the one which we are considering this rise of pressure is much more marked, and amounts to several atmospheres. If we look upon the pressure in the usual way as consisting of the sum of the partial pressures for the two constituents we can easily understand why the pressure should be higher the smaller the volume. The partial pressure for carbonic acid is equal to the vapour

pressure at 10°C . and therefore constant, but the pressure of the air becomes higher and higher, and the total pressure must therefore also rise with compression. Taken in this way the problem would be one of the absorption of a gas by a liquid, and of the validity of the laws of Dalton and Henry. But these laws, though capable of describing the phenomena in a few cases and under special conditions which need not be stated here, are as a rule inadequate, and more especially so the nearer one gets to the critical point. The problem must therefore be taken up in a different manner and the first step is to draw diagrams for mixtures in the same way as this was first done by Andrews for single substances. The changes of pressure and volume for our mixture at 10°C . are given diagrammatically in fig. 1 by the isothermal $t = 10^{\circ}\text{C}$. At b the conden-



sation begins, at e it is finished. The curve shows the rise of pressure in the gaseous state, a break at b , the rise of pressure between b and c , another break at d and a very steep curve beyond e in the liquid state. Curve $t = 25^{\circ}\text{C}$. shows the behaviour of the mixture at 25°C . This curve has no breaks. The mixture does not show any condensation and must evidently be above its critical temperature. Experiments have shown that the mixture cannot be condensed at temperatures higher than about 19°C . This temperature may therefore be called the critical temperature of the mixture, and it appears that the addition of one fifth of air has lowered the critical temperature considerably. In

compressing the mixture at a temperature below 19°C ., say at 18°C ., an entirely new phenomenon is observed. The liquid appears as at 10°C . at a certain volume (point *b* of the isothermal) and the pressure goes on rising after that; the liquid increases at first but its surface becomes less and less sharply defined and long before the whole of the mixture is liquefied the surface becomes a mist and disappears altogether in very much the same manner as the liquid surface of a single substance disappears at its critical point. On lowering the pressure the mist and the liquid surface reappear at about the same level where the disappearance took place before, and further lowering of the pressure gives the phenomena of compression in the opposite order. Similar phenomena are observed at lower temperatures, but the lower the temperature the larger the quantity of the liquid phase is when the surface disappears or reappears. Below 15°C . the whole of the mixture is liquefied, as described for the temperature of 10°C . If we call the disappearance or reappearance of the liquid surface in a mist the "critical phenomenon" we may express the experimental results by saying that the mixture shows the critical phenomenon not at one temperature only, but over a range of temperatures of about 4°C . (15° - 19°C .). By saying that 19°C . is the critical temperature for our mixture we evidently do not exhaust the phenomena. Above 19°C . no condensation takes place, but the critical phenomenon is not confined to that temperature but occurs at lower temperatures also. In fact as will appear presently the critical phenomenon really belongs to a temperature lower than 19°C . (about 15.6°C .) and it is in consequence of retardation and gravitation that it also occurs at temperatures up to the critical temperature.

Phenomena like those sketched were also obtained by Andrews with mixtures of carbonic acid and nitrogen, by Van der Waals with carbonic acid and hydrochloric acid, and others. Andrews' experiments are the most complete. He noticed great irregularities in the behaviour of his mixtures and thoroughly investigated their cause. He showed how they are explained by imperfect mixing of the

substances and great retardation in the establishment of the equilibrium in the long and narrow experimental tubes. If the mixture is partly liquid and is then compressed to a smaller volume, the pressure will be higher than it should be, and in leaving the mixture for some time at the same volume the quantity of the liquid increases while the pressure diminishes. If we start from a smaller volume and increase the volume the pressure will be too low and rises slowly while some more liquid evaporates. It takes a very long time for these changes to come to an end and it is very difficult without waiting hours at every change of volume to obtain concordant values at diminishing and increasing volume. Similar uncertainty attaches to the determination of the points *b* and *c* and of the critical constants. If the mixture is not homogeneous the critical temperature may be found several degrees too high.

Similar results were obtained by Ramsay and Young working with a mixture of alcohol and ether. Their investigation brings out the influence of retardation and imperfect mixing very strongly.

Some isothermals for mixtures of carbonic acid and sulphurous acid were obtained by Blümcke, but his experiments do not go as far as the critical region. Ansdell studied the condensation and critical point of mixtures of carbonic acid and hydrochloric acid. A number of observations regarding mixtures, especially critical temperatures, were made by Dewar. Unfortunately, several of the results obtained are doubtful in consequence of the influence of imperfect mixing of the substances.

Critical points of mixtures of liquids were determined by Strauss, Pawlewski, G. C. Schmidt, and others. Differences between mixtures and pure substances were not noticed: in fact the method of observation was, as a rule, one which did not allow either of a measurement of the pressure or of a change of volume.

The above remarks show in what way the experimental method had to be improved in order to get definite results independent of any retardation in the establishment of equilibrium. The little iron stirring-rod (if necessary, en-

closed in a small glass tube) which was applied by the writer of this article to obtain definite results at the critical point for so-called pure substances, as described in part i., was really devised for experiments on mixtures. This rod may be moved up and down inside the narrow tubes by an electromagnet which is outside the tube and the heating jacket surrounding it: it accelerates the process of mixing even at very large volumes, and enables one to obtain almost identical readings with diminishing and with increasing volume. But it is especially at smaller volumes and in the critical region that stirring is very effective. The critical phenomena obtained are practically free from retardation due to slow diffusion and differ materially from the phenomena as described by Andrews and others.

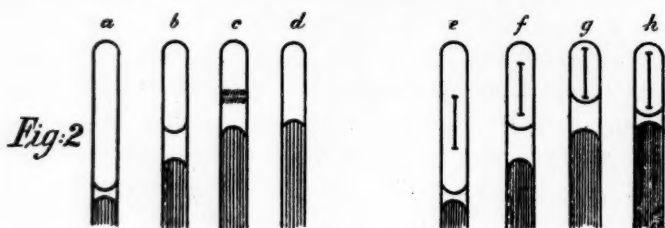


Fig. 2 (*a b c d*) gives the aspect of a tube containing our mixture of $5/6$ CO_2 and $1/6$ air at 18°C . at gradually diminishing volume without stirring as described above. In *a* the condensation has just begun, in *b* the liquid has increased and the liquid surface is flatter, in *c* the quantity of liquid is again more but the liquid surface is just in the act of disappearing (critical phenomenon), in *d* the mixture is homogeneous. Fig. 2 (*e f g h*) shows the behaviour of the same mixture at the same temperature (18°C .) but with stirring; *e* and *f* are very much the same as *a* and *b*, the surface, however, being better defined. In *g* the quantity of liquid *has passed through a maximum and is decreasing* with well-defined surface; in *h* the liquid is nearly all evaporated. No critical phenomenon takes place but a kind of condensation which is called "retrograde condensation" instead. Evidently the same would be found without stirring if one could afford to wait

hours or perhaps even longer. In diminishing the pressure the same phenomena are observed in the opposite order (*h g f e*). The higher the temperature the smaller is the maximum quantity of liquid, and at about 19° C. a minute quantity of liquid only just appears but disappears again immediately on compression. Though 19° C. may be called the critical temperature, because above 19° C. no two phases are possible, no "critical phenomenon" takes place there. If we follow the phenomena at somewhat lower temperature, say 17° and 16° , we find similar results; but the maximum quantity of liquid increases, while the liquid surface becomes less and less distinct. At last the liquid surface actually disappears, first near the bottom of the tube, and the lower the temperature the higher is the level at which it does so. At 15.6° C. it disappears in the middle of the tube, and it is below 15° C. that the liquid increases and fills the whole tube before the liquid surface disappears. The critical phenomenon is therefore confined to temperatures between about 15° C. and 16° C. From the theoretical explanation to be given below it will appear that the critical phenomenon really belongs to one temperature only, in this case 15.6° C.; a temperature which we shall denote as t_p . The fact of its occurrence at a range of temperatures (15° - 16° C.) is due to gravitation: the explanation is analogous to that given in part i. of the occurrence of the critical phenomenon for pure substances, at different volumes. In this case gravitation not only makes the density different at different levels but also the composition. As t_p depends on the composition x , *i.e.*, is different for different mixtures and, therefore, not the same for the mixtures at different levels in the tube, the critical phenomenon does not take place at the temperature t_p belonging to the mean composition x (here $5/6$) only, but also at temperatures slightly below and above t_p , each time at a different level in the tube. The longer the tube the wider the range of temperatures within which the critical phenomenon occurs. All this follows from the theory and is confirmed by experiment. If gravity did not act we should find normal condensation below 15.6° C., the critical

phenomenon at 15.6°C. (t_p), retrograde condensation with decreasing maximum quantity of liquid from 15.6°C. to 19°C. , and no condensation above 19°C. , the critical temperature t_c .

The same phenomena have been observed with a number of other mixtures, such as mixtures of carbonic acid and methyl chloride. The interval between t_p and t_c is however often much smaller than it was in this case. In mixtures of carbonic acid with acetylene and nitrous oxide with carbonic acid and with ethane the distance $t_c - t_p$ was so small that no retrograde condensation could be detected at all. These mixtures behave almost like single substances. This result may also partly be due to the action of gravitation which disturbs the real phenomena for mixtures in the way just described.

We are now in a position to complete the $p-v$ diagram for mixtures and consider in what respects it differs from the same diagram for single substances. The isothermal $t = 10^{\circ}\text{C.}$ was considered before. The curve shows two breaks at b and e : in experiments on mixtures of carbonic acid and sulphurous acid Blümcke found the isothermals continuous even below the critical region; this is due to retardation which tends to blur the discontinuities at b and e . On stirring the mixture the discontinuities reappear in the diagram. Through the different points b and e belonging to the isothermals at different temperatures we may as before draw a curve, the border or saturation curve. The isothermal for the critical temperature t_c is then found to touch the border curve, but not as for single substances at the top M of the border curve but at a point C to the right of M . The critical pressure is not the maximum pressure on the border curve. The isothermal for t_p , the temperature at which the mixture shows the critical phenomenon at P has a shape similar to the shape of the isothermal $t = 10^{\circ}\text{C.}$ Sometimes P is found on the left of M , sometimes on the right, and in exceptional cases it coincides with M . The isothermals which meet the border curve, must be supposed as for single substances to exist also inside the border curve and the same experimental facts exist to support this hypo-

thesis. Blümcke demonstrated the reality of the so-called theoretical isothermal for a mixture of carbonic acid and sulphurous acid by slowly expanding the mixture when wholly liquid and lowering the pressure below the pressures of the experimental isothermal; and in the same way by compressing the mixture carefully to a pressure above the pressure at δ . The writer of this article has often been able to confirm the former experiment.

The theoretical isothermal is given in fig. 1. as a dotted curve. It changes gradually into the shape above t_c . For single substances we saw the double wave shape disappear at the top of the border curve (here at M). At this point the critical isothermal for single substances has a horizontal tangent and the isothermals for higher temperatures have no points at which $\frac{dp}{dv} > 0$. For mixtures a similar transition takes place but now *inside* the border curve, as may be seen from fig. 1. The isothermals for temperatures just below t_c , though partly inside the border curve have no unstable part. The critical temperature, as it would be if the mixture remained homogeneous, is below the actual critical temperature.

It will also be noticed that the law for finding the border curve from the set of complete theoretical isothermals must be different from the same as explained for single substances. In that case the Maxwell-Clausius criterion solved the problem. Here the vapour pressure is a quantity which depends on the volume in consequence of the fact that the composition of the two co-existing phases is as a rule different. As was pointed out by Blümcke the area of the two surfaces inclosed between theoretical and actual isothermal must be again equal in this case. But this condition is evidently altogether insufficient for the solution; the complete solution will be given presently.

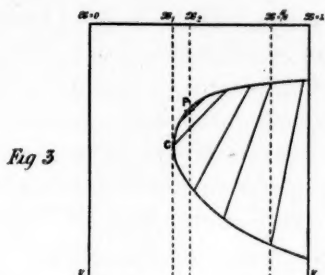
As regards the continuity of the liquid and vapour states the same remark may evidently be made as for single substances. A mixture in the condition of vapour may be changed into a liquid by a continuous set of changes.

There is no sharp distinction between one and the other any more than for pure substances.

An important question which presents itself is to find co-existing phases. In other words, what is the density (density is the reciprocal of the volume of a given quantity of mixture) and what is the composition of a liquid mixture in equilibrium with a vapour mixture? The liquid which during compression is formed when the condensation begins (at b fig. 1) has as a rule a different composition (as well as density) from the gas mixture. For our mixture of $5/6$ CO_2 and $1/6$ air the liquid will be much richer in CO_2 and only contain a small admixture of air. During the process of condensation the composition of both phases changes, as a rule in the same direction. For our mixture both the liquid and the vapour become poorer in carbonic acid, richer in air (this is not a misprint!). In the end when the whole of the mixture is changed into liquid its composition is again $5/6$, equal to the original composition. Our diagram (fig. 1) only gives us the density of the mixture at b where it is in equilibrium with a denser phase, a liquid, and e where the same mixture, but now itself in a denser state, is in equilibrium with a lighter phase, a vapour. But about the second phase, the liquid one which appears at b on compression and the vapour phase which disappears at e on compression or reappears on increasing the volume, the diagram does not say anything. We may find those phases however by combining the diagram with those for other mixtures of the same two substances. It is a result of thermodynamics, confirmed by experiment, that at given temperature and pressure there is only one equilibrium of two phases for a mixture of two given substances. The relative quantities of the two phases may be anything, but provided t and p do not change, the density and composition are always the same. Suppose therefore we take the isothermals for the same temperature (say $10^\circ\text{C}.$) for a number of mixtures of CO_2 and air and select that mixture x^1 for which the pressure at the point e , *i.e.* in the liquid state, is equal to the pressure at b for our mixture. According to the rule given above x^1 will be the mixture which co-exists at $10^\circ\text{C}.$ with the

mixture 5/6. The density is found at the same time. The same is true in general. We find sets of two mixtures which at the same temperature have the same saturation pressure, the one when liquid, the other when in a state of vapour. We may find in that way a number of pairs of phases which may co-exist, say at 10°C . and at different pressures.

A better insight is obtained by representing graphically the composition and density or volume of these co-existing phases. Fig. 3 gives the diagram thus obtained. The



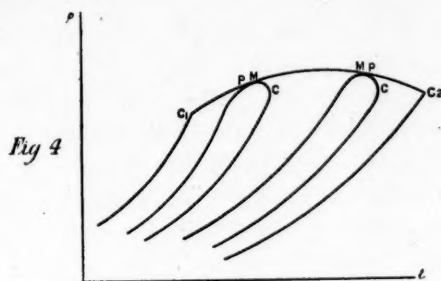
only values of x which are possible are those between 0 and 1 and the diagram is therefore enclosed between two parallel v axes and the x axis. The diagram is supposed to be drawn for 10°C . A curve is drawn through the co-existing phases and the corresponding pairs are joined by straight lines. To each of them belongs a different pressure. The pressure is lowest near $x = 1$ where in fact it approaches the saturation pressure of pure carbonic acid. It gets higher and higher towards the left hand side. The corresponding phases approach each other and finally coincide at P .

We may read the behaviour of any mixture of CO_2 and air at 10°C . from fig. 3 as far as condensation is concerned. A mixture for which $x = 5/6$ when compressed, *i.e.*, the total volume diminishing, shows liquid at b . The density and composition of this liquid is given by point c ; on being further compressed the two phases change. The straight line must be imagined to move towards the left and it may be proved that the relative quantities of vapour and liquid

present are given by the ratio of the parts into which b_c is divided by the stationary vertical line $x = 5/6$. The quantity of liquid increases until in e the whole mixture is liquid. Similar phenomena would be displayed by other mixtures. When, however, the composition x is less than x_1 (the line x_1 touches the curve in C) no condensation takes place. And for mixtures between the limits $x = x_1$ and $x = x_2$ (the line x_2 passes through P) the condensation will be found to be retrograde, the quantity of liquid reaching a maximum and diminishing until it is all evaporated. Mixture x_1 has its critical point in C, and 10°C . would therefore be the critical temperature for this mixture. Co-existence of two phases which approach each other and finally become identical must give rise to what was called the critical phenomenon and we see that at 10°C . this would take place for mixture x_2 . In order to return to the phenomena for a given mixture at different temperatures we have to draw the same diagram for those temperatures. It will then easily be seen that the phenomena obtained are exactly those which were described in the beginning. It is found that the critical phenomenon belongs to the one temperature t_p only if we do not take gravitation into account. In lowering the temperature the curve moves towards the left and at the critical temperature of air would touch the line $x = 0$. Below that temperature all mixtures would be condensable and no critical phenomena would exist.

Another instructive way of representing the experimental results is obtained by drawing the border-curves for the different mixtures in the p - t diagram (fig. 4), first studied by Duhem. The border curves have the shape of loops, in the simplest case lying in between the vapour-pressure curves for the two components. A curve may be drawn enveloping the loops. The points of contact P correspond to P in fig. 1 and fig. 3. The points C where the loop has a vertical tangent also correspond to the points C in figs. 1 and 3. The highest points of the loops (M) correspond to M in fig. 1. The difference between C P and M is clearly brought out by this diagram.

On the left hand side of the diagram P is to the left of M, on the right hand side P is to the right of M between M and C. But evidently t_c is always higher than t_p and t_m ; even when P lies beyond C on the lower branch of the loop as is sometimes the case.



By means of a diagram like fig. 4 we may predict with some certainty what the influence will be of an admixture of a substance a on another substance b . If the vapour pressure curve for a is above the vapour pressure curve for b the vapour pressure is likely to be raised by the admixture. We should also be able to say something of the influence on the critical constants, t and p , if we were able to enunciate a rule about the position and shape of the enveloping curve $C_1 P C_2$. This however is not the case. The critical temperature of a mixture is, as a rule, between those for the components, but the critical pressure has a tendency to be high for the mixtures and is often higher than for the pure substances. But both these rules, as also the rule that the loops lie inside the vapour-pressure curves, are far from general. The pressures for the mixture are in some cases higher, and in others lower than the vapour pressures for the components. Mixtures of this kind have been investigated by Konowalow, Guthrie, and others. The writer of this article found a maximum vapour pressure for mixtures of N_2O and C_2H_6 lying near $x = 1/5 N_2O$. This maximum was found to exist up to the critical region for these mixtures. Fig. 4 becomes complicated and, therefore, inconvenient in cases of this kind. As to the critical tempera-

tures, it was long supposed that the critical temperature for a mixture was always between the t_c temperatures for the components; Pawlewski and Strauss found it to be approximately proportional to the composition. This law does not take into account the difference between t_c and t_p , and is, moreover, found to be confirmed only in a few instances. Mixtures of CO_2 and CH_3Cl and of CO_2 and HCl do not obey the law, the deviations being several degrees, and higher for t_c than for t_p . Sometimes the critical temperatures for the mixtures are even partly outside those for the constituents. Mixtures of N_2O (36°) and C_2H_6 (32°) containing more than one-tenth of C_2H_6 have critical temperatures below 32°C . There is no reason why more instances should not be discovered, as so few accurate experiments have as yet been made in this direction. The critical pressures were between those for N_2O and C_2H_6 . The critical pressures for mixtures of CO_2 and CH_3Cl are some of them higher than for either of the substances. Evidently there is a great deal of variety. Pictet uses the determination of the critical constants (especially temperature) as a test for the purity of substances. It is obvious from the foregoing that this can only be a trustworthy method in very special cases where the nature of the impurity is known beforehand. A much better, but perhaps somewhat too delicate, test is the constancy of the condensation pressure, though again this method would fail altogether where the mixture was one of maximum or minimum vapour-pressure.

It is now necessary to point out the connection of the experimental results with the theory. In the above I have not followed the historical order. Before any accurate experiments were made, Professor van der Waals published a theory for mixtures without which the phenomena would not have been easily unravelled. It is not inconceivable that most of the results represented by our diagrams might have been arrived at by a long and laborious set of experiments, but practically it was the theory that led the way and even now there is a good deal in the diagrams which depends on the theory and is still waiting for experimental confirmation.

The theory assumes an equation of condition for a mixture analogous to the equation for single substances. Van der Waals uses the same equation for mixtures as he deduced for simple substances, *viz.* $\left(p + \frac{a}{v^2}\right)(v - b) = RT$ (1) but a and b now depend on the composition of the mixture x . Van der Waals finds

$$a = a_1(1-x)^2 + 2a_{12}x(1-x) + a_2x^2$$

and a similar equation for b ; a_1, a_2, b_1 and b_2 are the constants for the two components; a_{12} and b_{12} depend on the mutual actions. Equation (1) is an equation between p, v, T and x .

Now we may be perfectly assured that this equation is not correct. We saw how even for single substances the same equation fails utterly. But the general results of the theory do not depend on the special form of the equation. We only have to assume, as with single substances, the existence of some equation between p, v, x and T as describing the behaviour of the mixture under different circumstances. This equation should yield an isothermal with the double-wave shape at lower temperatures and no unstable parts at higher temperatures.

It has already been said that Maxwell-Clausius' criterion is not adequate to find the border-curve because of the different composition of the co-existing phases. This criterion was equivalent to the condition that the same number of molecules move from the liquid to the gas in the opposite direction. But as there are two substances the latter condition must now be applied to both. In thermodynamical language this double condition may be combined with the condition of the equality of pressure in the two phases into one condition. Van der Waals uses the condition in this form: in a given volume the free energy ψ ($\psi = \epsilon - \tau\eta$, ϵ = energy, η = entropy) is a minimum. One of the properties of ψ is $\frac{\partial\psi}{\partial v} = -p$.

In the case of one substance ψ is a function of v (at constant temperature). Below the critical temperature the ψ, x, v curve has a double tangent, the slope of which determines the vapour pressure, the two points of contact re-

presenting the co-existing phases. Points on the $\psi x v$ curve between those points of contact correspond to points on the theoretical isothermal inside the border curve.

For a mixture ψ is a function of v and x and may be represented by a surface the co-ordinates of which are ψ , v and x . Van der Waals proves that co-existing phases are now given by a double tangent plane. The surface presents a plait and in rolling over this plait the double tangent plane traces out on the surface the curve which represents the co-existing phases. This curve is called the connodal curve. Points inside this curve on the surface represent unstable or half-stable conditions of the mixtures, analogous to the points inside the border curve. If the corresponding points of contact approach and reach each other on that part of the surface which is inside the two planes $x = 0$ and $x = 1$ the plait is said to have a real plait-point; a plait-point is a point at which the co-existing phases become identical. If we project this connodal curve with its plait-point upon the vx plane we obtain the border curve in the vx diagram, in other words fig. 3. This diagram appears therefore in an entirely new light. P is now the projection of a plait-point and the curve the projection of a connodal curve. From the meaning of P as a plait-point it is clear that we may expect the critical phenomenon to be characteristic of that point. In general it appears that the study of condensation and critical phenomena may be identified with the study of the shape, position, changes and displacements of plaits and plait-points on the ψvx surface.

We are now able to sketch the method by which to find the border curves say in the $p v$ diagrams for the different mixtures. We must suppose the isothermals of a given temperature for a number of mixtures to have been determined. The equation of an isothermal may be written in the form $p = f(v)$. As $\frac{\partial \psi}{\partial v} = -p$ we can calculate, as is shown by Van der Waals, the ψ and draw the ψv curves for each of the mixtures. These ψv curves form together the ψvx surface. We then apply the double tangent plane and make it roll over the plait of the surface. The double

curve traced out by the points of contact gives the co-existing phases, and thus the volume at which any of the mixtures will be in equilibrium as a vapour with a liquid, or as a liquid with a vapour. In other words it gives the points b and c on the isothermals for the chosen temperature. By doing the same thing at other temperatures the border curves may be traced out in full. The results obtained may then be compared with the border curves, as found by actually observing the volumes and pressures at b and c .

A drawback of the $\psi v x$ surface is the indirect way in which the pressure manifests itself. The pressure depends on the slope of the tangent plane in the ψx plane. In general this slope changes continually in one direction during the motion of the tangent plane over the plait, and the maximum pressure is obtained at the plait-point P. This is not in contradiction with the distinction made between the points P (plait-point) and M (point of maximum pressure) in figs. 1 and 4. At M a given mixture has a maximum pressure on the border curve, or above that pressure no condensation is possible for that mixture. P on the other hand is a point of maximum pressure on the plait at a given temperature. At that temperature no mixture can exist in two phases at a higher pressure than belongs to P. But at a different temperature higher pressures may occur unless P and M coincide.

Sometimes the pressure on the plait, instead of rising or falling all the time, passes through a maximum or minimum. This occurs where there is a mixture of constant boiling-point. The co-existing phases have the same composition in that case, though different density, as was first demonstrated by Konowalow. It follows that the straight line connecting the corresponding points on the border-curve (fig. 3) is parallel to the v axis for that mixture. The straight lines on the two sides of the maximum or minimum line are spread out like a fan; the fan opens out in the direction of the positive v axis for a minimum, and in the opposite direction for a maximum. The latter case

occurs with nitrous oxide and ethane for a mixture containing about $1/5$ N_2O and $4/5$ ethane, as was already stated above. The fact was also mentioned that most of the mixtures of those two gases have critical temperatures below that of ethane. This is entirely explained by a splitting up of the plait before the critical temperature of ethane ($32^\circ C.$) is attained, at about $26^\circ C.$ Each of the halves of the plaits has its plait-point. In one of the halves the plait-point is situated as in fig. 3, *i.e.*, nearer the x axis than C. But in the other half, opposite the first, P lies farther away from the x axis than the critical point C. The critical phenomena which one may expect in that case are different from those described in connection with fig. 3. There are again the two temperatures t_p and t_c , but between them compression will give rise to the appearance of a second phase lighter than the mixture, therefore at the top of the tube. This vapour phase will first increase and subsequently decrease during compression. This new kind of condensation may be called "retrograde condensation of the second kind". Unfortunately, as was already stated, the temperatures t_p and t_c were so close that the critical phenomena were the same as if the mixtures had been single substances.

An important case which has not been considered is that in which the liquid phase itself is split up into two liquids, as in mixtures of water and ether, or water and carbonic acid, in other words the co-existence of two liquid phases and even of three phases, two liquid and one vapour. In cases of that kind the ψ *v* x surface has a second plait with properties similar to those of the vapour-liquid plait. If the connodal curves of the two plaits intersect, the tangent plane has three points of contact and therefore three phases will be in equilibrium. At each temperature there is only one pressure at which this triple coexistence is possible, and in the p - t diagram these corresponding values of p and t are represented by a curve. Besides this curve and the two vapour-pressure curves there are the border curves for the mixtures, which in this case have not the simple loop-shape (fig. 4), but form a kind of double loop owing to the

second plait. The theory may predict to a certain extent the various possible cases that may occur, but very little experimental work has as yet been done in this direction. Konowalow and Alexejeff's researches must be mentioned in this connection. Konowalow gives his results as curves in the $p x$ diagram, Alexejeff uses $x t$ curves. Both these diagrams are closely connected with the $p t$ diagram, because all three may be looked upon as sections of, and curves on, a surface, the $p x t$ surface. We might conveniently call that surface a "border surface" as it contains the phenomena of condensation, including the critical phenomena, for mixtures of two given substances.

The $p t x$ surface is obviously not the only border surface possible. Any three of the four quantities $p v t$ and x may be chosen as co-ordinates for a surface of that kind. A set of $v x$ border curves (of which fig. 3 is an example) would together give the $v x t$ border surface, and so on.

The same variety of choice exists if we want to represent by a surface the condition of mixtures when homogeneous, *i.e.* outside (or inside) the border curves. Blümcke has studied the properties of the $p v x$ surfaces for mixtures. None of these surfaces however gives the co-existing phases by a simple geometrical construction as Van der Waals' ψ surface does, and as long as the experimental data are so few as they are at present, it is highly advisable to take that surface as a guide and translate as it were its properties into any two or three dimensional diagrams which seem useful for our special purpose.

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J. P. KUENEN.

A REMARKABLE ANTICIPATION OF MODERN VIEWS ON EVOLUTION.

THE great pioneer of modern anthropological and ethnological research—James Cowles Prichard, was born at Ross, in Herefordshire, 11th February, 1786. The following brief account of his life is taken from Professor E. B. Tylor's article in the *Encyclopædia Britannica* (1885, vol. xix., pp. 722, 723). Prichard was brought up as a member of the Society of Friends, to which body his parents belonged. He joined the medical profession, taking his Doctor's degree at Edinburgh, "afterwards reading for a year at Trinity College, Cambridge, whence, joining the Church of England, he migrated to St. John's College, Oxford, afterwards entering as a gentleman commoner at Trinity College, Oxford, but seeking no degree in either University. In 1810 he settled at Bristol as a physician." Among his many great achievements in anthropology was the proof "that the Celtic nations are allied by language with the Slavonian, German, and Pelasgian (Greek and Latin), thus forming a fourth European branch of the Asiatic stock (which would now be called Indo-European or Aryan)". His treatise on the subject, entitled "*Eastern Origin of the Celtic Nations*," appeared in 1831. "It is remarkable that the essay by Adolphe Pictet, *De l'Affinité des Langues Celtiques avec le Sanscrit*, which was crowned by the French Academy and made its author's reputation, should have been published in 1837 in evident ignorance of the earlier and in some respects stricter investigations of Prichard."

Although Prichard's memory is much honoured, it appears that in one important respect he has not hitherto received his due. My friend Professor Meldola lately drew my attention to a section of the second volume of *Researches into the Physical History of Mankind* (2nd edition, 1826) which, as he pointed out, anticipated in the clearest manner the arguments which have been recently advanced

by Professor Weismann in favour of the non-transmission of acquired characters. The deep significance of the passages in question had been observed by Dr. Maurice Davis, J.P., who brought them under the notice of his son-in-law, Professor Meldola.

In response to Professor Meldola's invitation to prepare an account of this most interesting contribution to the history of evolution, I read the work carefully and soon found that other important ideas are anticipated in it.

Thus, Prichard apprehended with perfect clearness that domesticated races of animals and plants have been produced by the selection of man and not by favourable surroundings, careful training or cultivation. He believed in the possibility of organic evolution and supported it by excellent arguments which still have the strongest weight to-day. He even recognised the operation of natural selection although he assigned to it a subordinate rôle. The most important anticipation is, however, the masterly discussion on the transmission of acquired characters, a discussion in which the distinction between acquired and inherent or congenital characters is clearly drawn, and many of the most difficult cases are fully argued out, the conclusions reached being those independently arrived at by Professor Weismann over half a century later.

It is very remarkable that all this should have passed, as I believe, unnoticed. The neglect can only be explained by supposing that this particular edition was never consulted, but that Darwin and others always went to later editions of the same work. I shall be able to show that Prichard was not very confident in the strength of his own conclusions and, so far as I have consulted his later editions and works, I find reason for the belief that his convictions weakened still further. Indeed strong indications of uncertainty are to be found in the second edition itself, although they are confined to the later sections, and do not appear in close proximity to the important conclusions which they nevertheless affect.

It is certain that if Darwin had read this second edition he would have given Prichard a high place in the account

of the history of evolution which appears in the introduction to all later editions of the *Origin*. So too would my friend, Professor Osborn, have given high honour to Prichard in his interesting work, *From the Greeks to Darwin*. It is an anomaly that such works as the *Vestiges* should attract attention, while Prichard's keen insight, sound judgment, and balanced reasoning on many aspects of organic evolution should remain unknown.

I am very far from maintaining that these most interesting anticipations in any way diminish the credit of those recent writers who have treated the same subjects in greater detail and of course independently. The interest evoked by Dr. Davis' discovery in the literature of evolution is mainly due to the work of those recent authors by whom the whole subject has been brought into the light of day, and the attention of every intellectual man and woman has been compelled.

The limits of space oblige me immediately to proceed, after this too brief introduction, with a detailed statement of Prichard's arguments and conclusions, which will be found to justify, in the fullest manner, all that I have said in his praise.

It has already been said that the arguments referred to are found in the *Researches into the Physical History of Mankind*, vol. ii. (London, 2nd edition, 1826). They are included in the seven sections of the first chapter of Book ix (p. 525), which is entitled a "General Survey of the Causes which have Produced Varieties in the Human Species, with Remarks on the Origin of Nations and on the Diversity of Languages". The first chapter treats "Of the Causes which have Given Rise to Varieties in the Human Species". In the first section of the first chapter the author admits that it is fruitless to seek for a complete explanation of the causes which have produced the varieties which are witnessed in the human species. "The origin of the varieties in the breed is enveloped in the same obscurity which still hangs over every question relating to the theory of propagation."

The opinion that the different shades of colour met

with in various races are caused by climatic changes and by varying intensity in the rays of the sun, is then considered, and a great many ancient and modern exponents of this view are quoted. After reproducing a long passage from Buffon, the hypotheses of the Rev. Dr. S. S. Smith of New Jersey are described. These deal not only with the "gradation in the complexion nearly in proportion to the latitude, . . ." but also with the influence which heat exerts upon the secretion of bile. In consequence of heat "the bile . . . is augmented. . . . This liquor tinges the complexion. . . ." "Bile, exposed to the sun and air, is known to change its colour to black—black is, therefore, the tropical hue." This latter and the very similar views of Blumenbach are, however, dismissed by Prichard as "without foundation"; while as to the former suggestion of Dr. Smith, together with that of Buffon and the older writers, he observes that the principal observations on which it is based are correct. "It is certain that the majority of black races of men are inhabitants of the intertropical regions, and that most of the light-coloured nations are to be found in cold or temperate climates." But although he admits the fact, he maintains that it is capable of "a different interpretation from that which modern writers have in general adopted". He similarly admits that the skin of a European is darkened by the sun, and continues: "It seems, at first, not very improbable that individuals darkened by exposure to heat in southern climates, may have an offspring of deeper colour in consequence, and if this effect increases in every generation it may be thought sufficient, in a long course of ages, to produce a black colour of the deepest tint". But this view does not by any means commend itself to him; for he continues "that this notion, however, is altogether incorrect, I venture to conclude from the following considerations:—

"1. The progeny of individuals, embrowned by exposure to the sun, is born with the original complexion, and not with the acquired hue of the parents." Furthermore, he points out that white and black races moved respectively to tropical and temperate climates have retained their original colour for ages. The second consideration which leads him

to reject the above-mentioned conclusion is very significant, and I give it in his own words (p. 532):—

“2. The supposition is contrary to a general law of the animal economy, according to which, acquired varieties are not transmitted from parents to their offspring, but terminate in the generation in which they have taken their rise.”

The succeeding two sections are allotted to the considerations contained in paragraphs 1 and 2.

Section ii. (p. 532) is headed “Instances Showing the Permanency of Complexion in Different Races”. The cases in which races have completely changed in colour after removal to a different climate he explains by a mixture of breed; and points out that “it is easy to find examples of an opposite tendency, and to show that the original hue has been preserved” Thus he brings forward the instances of the descendants of English colonists in the West Indies and Spanish in South America who “remain as fair as their European ancestors,” when there has been no intermarriage with other races. “That this assertion is correct, I am convinced,” he says, “by the results of repeated inquiries.” In the East the same results are found, although the migration of white races into hot climates took place at far earlier dates. Thus amongst other examples he mentions that of the “white or Jerusalem Jews” who are believed to have migrated to the Malabar coast in the year 490 A.D., and whose living descendants are “said to resemble the European Jews in features and in complexion”.

The converse “experiment of transplanting black races into northern climates” has not been carried on for so long a period, but Dr. Prichard points out that “several generations have produced little or no alteration in the complexion of Negroes in the United States and in other temperate climates”. It is indeed stated that “the domestic Negroes who are protected from the heat of the sun by more clothing, and who pass their time in sheltered houses, are of a darker complexion than the slaves who labour half naked in the fields”.

Section iii. This most significant and remarkable part

of the work is headed (p. 536), "Laws of the Animal Economy in Regard to the Hereditary Transmission of Peculiarities of Structure"; the brief title at the head of the pages runs "Laws of Nature in Hereditary Transmission". This discussion, which forestalls by more than half a century the considerations and conclusions of recent writers and especially of Professor Weismann, is opened by the statement that physiological writers have often inquired "what peculiarities of structure are liable to be transmitted by parents to their offspring, and what terminate with the individual without affecting the race. Perhaps the following remark," the author goes on to say, "may afford the solution of this inquiry".

I must now quote without any omission the succeeding two paragraphs in which the two classes of characters—inherent and acquired—are defined, as fully and clearly as they have ever been, and the opinion is strongly expressed that the former are transmissible, the latter non-transmissible by heredity:—

"It appears to be a general fact, that all connate varieties of structure, or peculiarities which are congenital, or which form a part of the natural constitution impressed on an individual from his birth, or rather from the commencement of his organization, whether they happen to descend to him from a long inheritance, or to spring up for the first time in his own person—for this is perhaps altogether indifferent—are apt to re-appear in his offspring. It may be said, in other words, that the organization of the offspring is always modelled according to the type of the original structure of the parent."

"On the other hand, changes produced by external causes in the appearance or constitution of the individual are temporary, and, in general, acquired characters are transient; they terminate with the individual, and have no influence on the progeny."

At this point the author adds a most interesting footnote in which he tells us (p. 537) that "this distinction, which has not been pointed out by any former writer on physiological subjects, was first suggested to me in conversa-

tion many years ago by Mr. Benjamin Grainger, of Derby". It would be of high interest to ascertain something more about Mr. Grainger and to find out whether he ever published on his own account. It is however probable, from the other pregnant ideas contained in Dr. Prichard's work, that the clear expression, apt illustration, and admirable discussion of these principles are entirely original.

He then proceeds to illustrate the first proposition "that all original or connate peculiarities of body are hereditary"; first instancing the well-known "porcupine family, in which a remarkable peculiarity of the [human] skin was transmitted through three successive generations," and the facts which prove the hereditary nature of complexion, as shown in section ii. Supernumerary and abnormally thickened digits are then brought forward and proved by many examples to be markedly hereditary; as also "a singular thickness of the upper lip, in the Imperial house of Austria," introduced it is believed "many centuries ago . . . by an intermarriage with the ancient house of Jagellon".

The last examples of such connate characters are especially significant. "The same observation equally applies to those minute varieties of organization, which give rise to peculiarities of habit or temperament, and predispose to a variety of morbid affections, as deafness, scrofulous complaints, and the whole catalogue of disorders in the nervous system. Even those singular peculiarities termed idiosyncrasies are often hereditary, as in the instance of a remarkable susceptibility of the action of particular medicines, such as mercury."

With regard to the second proposition "that acquired peculiarities, or characters impressed by adventitious circumstances, and not arising in the spontaneous development of the bodily structure, are never transmitted . . ." he remarks, as it has often been insisted upon since, that the conclusion "is more difficult to establish than the foregoing . . ., since the proofs must needs be of a negative kind. But," he continues, "there is no want of evidence of this description." And he again insists, as if he could not put it

too clearly and emphatically: "It seems to be the law of the animal economy, that the organization of the offspring, which as we have seen follows the type given by the natural and original structure of the parent, is unaffected by any change the latter may have undergone, and uninfluenced by any new state it may have acquired".

He then discusses the examples which are supposed to support the opposite conclusion, first mentioning the statement "that dogs and cats, the tails of which had been cut off, sometimes produce young ones which have a natural defect of the same part. It is taken for granted that these appearances are connected together in the relation of cause and effect, and therefore afford a proof that acquired peculiarities are hereditary." The author argues that cases of this kind are accidental, and he points out that such defect of parts is apt to occur in every species;—in man as well as in animals. He points to the vast experiment due to "our caprice" in mutilating the ears and tails of domestic animals, and to the effects of surgical operations upon man. What remarkable results would be witnessed if such changes were hereditary!

Professor Weismann was first led to the same conclusion as Dr. Prichard by constructing a theory of heredity which seemed to him to explain the facts and observations better than any which had been previously proposed. But the theory did not include any mechanism by which the transmission of acquired characters could take place. Professor Weismann, believing that his theory was in the main right, began to inquire for the evidence on which the belief in such transmission is based, and as soon as he commenced his inquiries the evidence broke down in every direction.

With Prichard it was otherwise, for the existing theories seem to have been against him. Thus he argues that his opponents "seem to have derived their opinion rather from some conjectural theory of generation, than from any facts which have appeared well established"; and he goes on to contend that we know so little "that we are not authorized to reason from any hypothesis on this subject".

He next deals with the statement "that after mutilation or other artificial change has been repeated through many

generations, a sort of habit may be acquired, by which the new state becomes as it were natural, and may thus modify the race". To this he replies that the evidence of such habit could only be obtained by diminishing the mutilation in progressive generations and comparing the result; whereas in all such cases the violence committed and the resulting injuries are continued unabated. "If, however, an experiment be wanting to prove that repetition effects no difference in the results," he points to the practice of circumcision which has gone on for some thousands of years without producing any hereditary change.

Prichard argues that such non-transmission is beneficial, in fact he contends "that all the laws of nature, or the general plans which we trace through the organized world, tend uniformly to produce beneficial effects, though *particular* evils are sometimes *contingent* upon their operation". With regard to this instance he points out that, if such transmission took place, both man and animals would practically become more and more "mutilated and defective".

The author next proceeds to consider the effects of disease, introducing the subject in the following paragraph: "we cannot discern any essential circumstance in which changes produced by art or by casual injury differ from those which are effected by other external causes. We should therefore suppose from analogy that the latter are not more communicable to posterity than the former, and this presumption is confirmed when we inquire into facts."

He points out that the constitutional effects of many diseases ("small-pox, measles, scarlatina, whooping-cough"), rendering those who have suffered from them more or less immune, are never hereditary. Without attempting to explain in what the change consists, he rightly claims it as "a permanent state of the constitution, which lasts as long as the individual. . . . Those imperceptible modifications in the bodily structure which render the constitution incapable of being acted upon by certain morbid poisons are governed by the same law, as far as regards hereditary descent, as the observable changes of form which are induced by art or accident."

At this point the writer intercalates another clear statement of the essential distinction between inherent hereditary and acquired non-hereditary characters. The statement is so admirable that I quote it in full.

"We may remark in general that each individual being, through the animal and vegetable worlds, has certain laws of organization impressed upon its original germ; according to which the future development of its structure is destined to take place. These inbred or spontaneous tendencies, governing the future evolution of the bodily fabric, cause it to assume certain qualities of form and texture at different periods of growth. From these predispositions are derived the characteristic differences, and the peculiarities of individual beings. Now it appears that such spontaneous tendencies are alone hereditary, and that whatever changes of organization are superinduced by external circumstances, and are foreign to the character of structure impressed upon the original stamina, cease with the individual, and have no influence on the race."

"Yet this law of hereditary conformation exists with a certain latitude or sphere of variety, but whatever varieties are produced in the race, have their beginning in the original structure of some particular ovum or germ, and not in any qualities superinduced by external causes in the progress of its development."

These sentences might well have been written to-day, to sum up the results of all our observations on such subjects. These results have been summed up at greater length and in more technical language, but I venture to think that Dr. Prichard's statement contains everything that is valuable and essential in every later attempt. It will be observed that Weismann's conception of inherent characters as blastogenic, acquired as somatogenic, stands out clear and distinct; furthermore, that the source of individual difference is traced to the germ.

After these general statements he returns to the question of disease and discusses predisposition. He points out that medical writers have generally believed that any predisposition to disease may arise in any constitution if subjected to

the appropriate causes ; " that . . . the gouty diathesis, for example, may be acquired by long habits of intemperance, and transmitted to posterity," and so also with other ill effects witnessed in the children of dissolute parents. If this be so, Prichard admits that " we have a clear proof of the hereditary nature of acquired states of the constitution".

Against such a view he contends that any particular disease can only follow when there exists " a preparation, laid in the first place by nature, in the original stamina and habit of the body"; and he points out that the same hurtful cause may produce quite distinct diseases. Thus " intemperate living . . . is commonly said to bring on, in one person, a predisposition to gout, in another to diseases of the liver, or of the stomach, or of the brain. Now since the difference is not in the external causes, it must be in the natural peculiarities of the constitutions on which they act. These, therefore, are previously fitted by original organization to take on them one form of morbid affection rather than another. It is then clear that the predisposition is laid by natural or congenital structure, in the first instance." Individuals differ in particular organs; the exciting causes of disease bring out the weaknesses which previously existed and might otherwise have remained unknown. Such defects " being a part of the original bodily structure" are hereditary. " The first individual who exposes himself to the morbid causes, first betrays the peculiar defect of his race, and is thus erroneously supposed to lay the foundation for it."

Syphilis, which appears to be an exception, he explains by " a peculiar mode of infection. . . . This is evidently a phenomenon of a very different kind from the similarity of structure which the laws of nature have ordained between parents and their offspring."

Hence he infers " that the phenomena of predisposition to diseases, rather confirms than invalidates the general observations before laid down, and we may be allowed to conclude, that no acquired varieties of constitution become hereditary, or in any manner affect the race".

The preservation of complexion after a race has migrated to a very different climate conforms to the general law. Although the parents may alter greatly "the adventitious colour has no influence on the offspring".

Hence in looking for the causes of varieties of mankind we must not "direct our attention to the class of external powers which produce changes on individuals in their own persons, but to those more important causes, which acting on the parents, so influence them that they produce an offspring endowed with certain peculiar characters, which characters, according to the law of nature, become hereditary, and thus modify the race".

The sentence I have last quoted concludes the section and very naturally introduces section iv., entitled, "Theory of the Origin of Varieties" (p. 548).

This section opens with a sentence which might well have been written by Darwin: "Varieties of form or colour, as they spring up in any race, are commonly called accidental, a term only expressive of our ignorance as to the causes which give rise to them". On the other hand—"how, by what influence, and in what manner" they are produced, "we shall perhaps never be able to ascertain".

Examples of new varieties which have sprung up within the experience of man are then given: the "porcupine" and six-fingered man, albinos and variations in colour. He next describes the sudden origin of the ancon or otter breed of sheep, quoting from Col. Humphries in the *Philosophical Transactions* for 1813 (part i.).

Prichard favours the view that when the offspring does not exhibit a new variety but follows the main lines of its race or breed, it is apt to be influenced by the father rather than the mother; and he quotes a number of statements and opinions believed to favour this view; and finally alludes to the celebrated cross between the mare and the male quagga in which it was confidently believed that so great an effect was produced on the former that her later offspring, although begotten by a stallion, were influenced in the direction of the quagga (telegony).

The mother, on the other hand, was believed to be in

the main responsible for the new varieties which arise from time to time. This opinion Prichard considered to be probably well grounded; and the conclusion that size and stature chiefly depend on the mother he also thought to be well established. Hence we see that his judgment and penetration were not always proof against popular convictions insufficiently sustained by evidence. These strange views about the relative importance of the two parents seem to have disappeared, and only traces of them are to be found in the popular beliefs of the day.

The author dismisses the extreme cases of the supposed effect of the mother's imagination upon the unborn child as manifestly absurd; but looks with some favour upon the opinion, also held by Erasmus Darwin whom he quotes, that the future offspring may be effected by the imagination of the parent at the moment of conception. In proof of the ancient origin of this belief he alludes to Jacob's experiments upon the flocks of Laban.

When, however, Prichard comes to reconsider all his suggested causes of variation he is dissatisfied with them and admits that "the circumstances—are of a more permanent nature," and that it is often "impossible to discover any peculiar circumstance in the condition of the mother". This leads him to consider the similar instances among domestic animals and among plants and at this point he anticipates in a truly remarkable manner Darwin's general conclusions as to the origin of our domestic breeds.

"It is generally supposed," he says on page 557, "that cultivation is the most productive cause of varieties in the kind, both in the animal and vegetable kingdom. But it may be questioned, does cultivation actually give rise to entirely new varieties, or does it only foster and propagate those which have sprung up naturally, or as it is termed accidentally?"

"In this latter way the influence of art is very important in constituting breeds, as of cattle, dogs, horses. The artificial process consists in a careful selection of those individual animals which happen to be possessed, in a greater degree than the generality, of any particular characters

which it is desirable to perpetuate. These are kept for the propagation of the stock, and a repeated attention is paid to the same circumstances, till, the effect continually increasing, a particular figure, colour, proportion of limbs, or any other attainable quality, is established in the race, and the uniformity of the breed is afterwards maintained by removing from it any new variety which may casually spring up in it."

The main result of Darwin's indefatigable labours on the formation of domestic races could not be more accurately summarised than in these words published in 1826.

Prichard expresses himself as uncertain whether domestic animals are more prone to vary than others, but considers that the artificial conditions may in all probability "occasion deviations in their progeny".

The influence of climate seemed to him the most important of all causes of race-formation—so important in fact that he discusses its examples under a separate section, while the adaptation of races, animal and human, to their climates form the subjects of the concluding sections vi. and vii.

The examples of the effect of climate are brought forward in section v. (p. 558), entitled, "Instances of Variety in the Breed, Arising from the Operation of External, Chiefly of Local Causes". The first instance is that of the swine of Cuba which are said to be twice the size of the parent breed. He then instances the peculiar and uniform colour of the cattle and horses "descended from the variegated domestic breeds" which have become wild in South America, and the common bear which differs in colour in various European localities.

When the races of several distinct species resemble each other in a single locality it is fairly maintained that some special local influence may be strongly inferred. Thus it is stated that the Angora breeds of rabbits, goats, and cats are remarkable for their long fine silky hair and white colour. "These characters . . . indicate a common cause, which must be some peculiarity in the circumstances under which these animals exist in the climate and situation occupied by them."

Then follow many other examples—the blackness which characterises both men and animals in Malabar and Guinea, the whiteness of Polar animals, the height of Patagonian man, the differences which separate the English race in America and the West Indian Islands from that in the parent country, and the negroes of America from those of Africa.

The section concludes in a significant paragraph in which the author suggests that perhaps some of these local varieties may be specially adapted to “the circumstances of the countries in which the deviation has taken rise,” and he finally concludes by introducing the succeeding section in these words: “It may indeed be inquired, whether the deviations in general, which appear to follow a change of climate, are not founded on a law of the animal economy, which gives rise to an alteration in the breed calculated to fit the race for its new abode” (page 566).

The sixth section (p. 567) is headed “Adaptation of Certain Breeds to Particular Local Circumstances”. In this section we are provided with numerous instances of the adaptation of races to their environments. Blumenbach’s opinion in favour of the multiple origin of the dog is quoted at some length. Considering the undoubted adaptation of many breeds for certain ends this naturalist concludes: “I can scarcely persuade myself to look upon this as a mere accidental consequence of degeneration, and not rather as an intentional contrivance of the wise Creator”. To this Prichard replies that such a remark “suggests the inquiry whether the degeneration or variation of animals is in fact a mere accidental phænomenon . . .”. We should note that degeneration is here used in the sense of departure from ancestral type, and not implying, as it does in our time, any degradation or simplification of structure.

Then follows a paragraph most significant of modern views of organic evolution and the kind of evidence on which the modern naturalist relies. The remarkable “double relation” which individual species bear on the one hand to their special localities, and on the other to the group to which they belong, is first pointed out, and main-

tained to be characteristic of the vegetable kingdom as well as the animal. Thus the species of a family or genus are often distributed round a centre "which seems to be the principal focus or favourite seat of the tribe," from which the branches diverge in various directions. The particular species, when compared, can be referred to "one type of organization". The slighter differences between them "seem to lose themselves in the sameness of form belonging to the genus, and even suggest a suspicion that they all proceeded from one original. The phænomena of resemblance must have had their sufficient reason as well as those of diversity." He then inquires whether the explanation is to be found in the action of "some slight modification in the productive causes" which stamped the genus at its first appearance "with all these specific diversities"; or whether on the other hand a uniform genus was first created which "afterwards became diversified by the influence of external agents". He concludes that the former of these alternatives is more strongly indicated by the knowledge of his time.

"Whichever of these suppositions may be true in point of fact, the separation of families and genera into particular species, and the distribution of these species to particular habitations, according to their physical properties, is evidently a part of the provision of nature for replenishing the earth with organized inhabitants, placed everywhere according to the congruity of soils and temperatures, with their structure and habitudes.

"But why is it to be supposed that the influence of this law of adaptation has stopped here? Is it not probable that the varieties which spring up within the limits of particular species, are further adaptations of structure to the circumstances under which the tribe is destined to exist? Varieties branch out from the common form of a species, just as the forms of species deviate from the common type of a genus. Why should the one class of phenomena be without end or utility, a mere effect of contingency or chance, more than the other?

"There are indeed many instances in which we can

perceive an advantage in the varieties of form, and an adaptation of particular breeds to external circumstances." He then gives numerous examples—the small active cattle and horses which are found in mountainous countries, the larger forms which flourish on fertile plains; the various breeds of the hog which are believed to hold "a particular relation to the localities in which they are placed"; the change of a thick fleece into a thin coat when certain breeds of sheep are transported to the tropics. "On considering these and analogous phenomena, we can scarcely avoid concluding that the variation of animals proceeds according to certain laws, by which the structure is adapted to the necessity of local circumstances."

This statement looks at first sight very much like natural selection. It is clear however that the writer held a view similar to that which has been termed "self-adaptation" by some modern writers, *viz.*, that external influences act on the organism in such a manner as to evoke directly a favourable response.

Examples of similar adaptation are then found among the races of man. The skin of black races is considered to be a protection against the effect of heat; the native African races can multiply in localities where a white population cannot maintain its numbers, while negroes are unable to establish themselves in northern latitudes. From these and many other instances, it appears that "in mankind, as in some other races, particular varieties are adapted by constitution and physical peculiarities to particular local situations".

The section finally concludes with the following paragraph: "These remarks, if they are well founded, serve to illustrate the doctrine of variation, or deviation, in the races of animals in general, and they seem to lead us to the conclusion, that this is not merely an accidental phenomenon, but a part of the provision of nature for furnishing to each region an appropriate stock of inhabitants, or for modifying the structure and constitution of species, in such a way as to produce races fitted for each mode and condition of existence. A great part of this plan of local adaptation appears to have been accomplished by the original modifi-

cation of a genus into a variety of species. It has been further continued, and the same end promoted, by the ramification of a species into several varieties."

The seventh and last section (p. 575) of this part of the work treats "Of the Relation of Particular Varieties of the Human Species to Climates".

Prichard evidently thought that adaptation of races to climate is especially characteristic of the human species, and must be admitted to hold in certain instances whatever be thought of his hypothesis that "the varieties in the species of animals proceed from a principle in nature, modifying the structure and constitution of races, and adapting them to the physical circumstances under which these races may be destined to exist . . .". He considers that the distribution of the races of men bears "a certain relation to climates," and gives a broad sketch of the geographical arrangement of races in support of this opinion. At the conclusion, after inquiring how it is that "these varieties are developed and preserved in connection with particular climates and differences of local situation," he gives the following very significant answer: "One cause which tends to maintain this relation is obvious. Individuals and families, and even whole colonies, perish and disappear in climates for which they are, by peculiarity of constitution, not adapted. Of this fact proofs have been already mentioned." We have here the undoubted recognition of natural selection, and it is remarkable that a man of such penetration who recognised fully that domestic breeds are due to man's selection, should not have seen in this principle a larger importance and have extended it to the relations of species to each other as well as to their physical environment. Great as Prichard was he did not appreciate the most pressing part of the "struggle for existence".

Prichard furthermore considers it probable that there are local influences which "promote the appearance of those varieties which are best suited to them, or tend to give rise to their production in the breed". He freely admits that this conclusion conflicts with his contention in section ii., that the colour of a race is not permanently

affected by a change of climate, and, he might have added, conflicts equally strongly with his argument in section iii., that acquired characters are not transmitted. However, he is so fascinated by the view of a local influence directly producing adaptation that he throws over much that he had previously argued for in a most convincing manner. Thus he suggests that races of men when removed into another climate may not change because they are defended from the local influences by living in houses, adhering to their old foods, etc., also that the facts about the black and white Jews of Cochin, from which he argued in section ii. that climate produces no permanent effect on the race, may be insufficiently known.

It is strange that one who reasoned so acutely in section iii. did not seem to see that the following view if proved to be true would undermine the whole of the argument: "It may however be true, that particular varieties, once established in the stock, and transmitted for many generations, though originally resulting in a certain degree from the influence of local causes, will nevertheless continue permanent, even long after the race has been removed from the climate in which they originated".

In spite of this logical flaw, which is in itself of much interest, inasmuch as it probably explains the suppression of Prichard's original views in later works, sufficient has been said to prove that the author was one of the most remarkable and clear-sighted of the predecessors of Darwin and Wallace.

E. B. POULTON.

THE DISEASES OF THE SUGAR-CANE.

PART I.

IN a preceding paper, the present economic position of tropical sugar-growing countries was passed under review. Attention was directed to the unequal conflict taking place between cane sugar and bounty fed beet sugar for the possession of the market of the world. And it was pointed out that the British West Indian Colonies, unsupported by any form of protection, are quite unable to meet the strain, and appear to be on the verge of bankruptcy.

It would have seemed incredible a few years ago that the cane would ever be replaced by its inferior rival, the beet-root. But the latter owes its present predominance in a measure to this very inferiority. The taxing of Colonial sugars gave the beet growers a chance, and all the resources of modern science were brought to bear upon the improvement of their staple. The problems to be solved were mainly botanical and chemical. It was necessary, by careful selection, to obtain varieties with richer juice, and, by improved processes, to extract a maximum of the sugar in this juice. As a result, the beet-root of to-day is little inferior to the cane as a sugar producer, while the processes of extraction and purification are well nigh perfect.

The fate of cane-growers, tied to their old mills, with their 50 per cent. to 60 per cent. extraction, and 40 per cent. to 50 per cent. waste, is certain; but there is still fight in those equipped with new and improved machinery, worked on a large scale.

2. In view, however, of the successive phases in this great economic struggle, there is a danger of losing sight of facts of another and equally important class. In a great many estates, whether poorly or well equipped as regards machinery, the cane juice is found to be of very inferior quality; and this becomes more marked as crop proceeds. The quantity of sugar produced from areas of the same size rapidly diminishes as the season advances, and it be-

comes necessary for the machinery to be worked night and day to prevent serious loss. The cause of this decrease is that the canes are infested by animal and vegetable parasites which increase enormously as the canes ripen. It becomes literally a race between the mill and the cane pests as to which shall appropriate the spoils of the fields. Disease is spread abroad in the estates, changing the delicious juicy canes into vinous and putrid masses. Let us glance at the state of the plantations in different parts of the Tropics.

3. Java, one of the largest and most successful of cane-growing countries, is saturated from one end to the other with *Sereh*, a disease which, after years of close study, has much in it still to puzzle the plant-pathologist. As in many other maladies, there are all degrees between perfect health and pronounced disease, and it is difficult to mention any one characteristic symptom. In severe cases, instead of the normal formation of long healthy joints, the plants become stunted, the canes are arrested in their growth and remain short, while the lateral buds, usually flat and "sleeping," swell and grow out. A bush-form is thus arrived at, more or less resembling that of "sereh" the common lemon-grass (*Andropogon Schoenanthus*).¹ The root-system is poorly developed and diseased at the tips; and what food materials find their way into the stem are diverted from the cane to the bursting lateral buds. In such a plant the fibrovascular bundles are seen to be red in colour, especially at the junction of leafsheath and node;² the large vessels are filled with gum which contains immense numbers of bacteria. Obviously this must interfere with the water supply; but it seems probable that the bacteria are mere accompaniments of the disease.

It is difficult to form an idea as to the actual loss inflicted on the island by sereh. One writer has calculated that in 1889 the diminution of crops in Mid Java alone represented a loss of two and a half to five million gulden (£200,000 to £400,000?).³ A more recent estimate, based upon

¹ Krüger (1) p. 126.

² Went (1) p. 470.

³ May.

circulars sent out during 1896, places the annual loss as 4·83 per cent. of the crops (equal to about £220,000?).¹ Besides the sereh, quite a number of parasitic fungi have been described as attacking the leaves and stalks of Java canes, ranging from harmless saprophytes to active and dangerous parasites.²

4. The sugar-growing districts of Queensland and New South Wales, although but recently established, have their full share of animal and vegetable parasites. Most destructive of these is the *Gumming*, thus described by the government pathologist.³ If, as in slight attacks, a "cane" is formed, cavities appear inside the tissues at the top of the stalk, filled with offensive matter, and accompanying the death of the apical tuft of leaves. Where the attack is severe, plants reach the height of one or two feet, and then die back, shooting out again from the base and forming buds half way down the stalk. The vessels, if examined, are found to be full of gum, and this, under high powers is seen to be swarming with bacteria. As a result of careful inoculation experiments, the disease of gumming has been attributed to the bacteria (*Bacillus vasculorum*) which produce the gum and cause the stoppage of the vessels.⁴ While offering many points of similarity with sereh, the Australian disease is readily distinguished by the exudation from cut surfaces, of a clear, yellow mucilage which leaves a bright stain on drying. Gumming is also reported as serious in Mauritius⁵ and Pernambuco, the sugar-growing province of Brazil.⁶ The latest reports show that this bacterial disease has gained a footing in Java, although at present only found in one or two, strictly isolated spots.⁷

5. The cane-fields in the West Indies are being devastated by a parasitic fungus, recently described as *Trichosphaeria Sacchari*,⁸ and locally known as the "rind fungus". In this case the plants frequently grow luxuriantly, and fine, stout canes with good joints are formed. As the time for cutting the canes approaches, to the despair of the planter,

¹ *Archief*, p. 612, 1896.

² Wakker and Went.

³ Cobb (1).

⁴ Cobb (2).

⁵ Boname (1).

⁶ *Sugar-Cane*, 1897, xxvi., p. 377.

⁷ Went (2).

⁸ Massee (1).

discoloured patches appear upon the joints halfway up the stem. The tissues beneath these spots are seen to be red or brown, and are found to have lost their sweet taste. Examination under the microscope shows the cells to be penetrated in all directions by the hyphæ of a fungus. A little later, black eruptions are noticed on various parts of the stem, especially near the tips of the sleeping adventitious roots, which form a zone at the base of each joint. Fine, curled, black threads are emitted at these points. A microscopic examination of these threads reveals countless conidia united together by a mucilaginous matrix. This is the common or *Melanconium* stage of *Trichosphaeria Sacchari*. The disease is particularly harassing because it does not declare itself till the year's agricultural work is done and there is the promise of an abundant harvest. It spreads with incredible rapidity, and the canes, if not immediately cut, fast deteriorate, until, in bad cases, they are not worth the cost of reaping.

6. In all parts of the Tropics, further, there are numerous animal parasites on the canes. It is difficult to give an idea of their numbers or to form an estimate of the damage inflicted by them. Occasionally one of them increases to the proportions of a plague—witness the locusts of the present season in Natal—but their destructiveness just now seems to be secondary to that of the fungoid and bacterial diseases. There remains much to be done before our entomological knowledge of the cane-fields is at all complete. Here and there detailed studies have been commenced; and there seems some prospect of this being continued in East Java, where an entomologist is attached to the Experimental Sugar Station. One author enumerates between sixty and seventy species of insects known by him to be injurious in the Java cane-fields: six beetles, six "borers," twenty-five other grubs, several grass-hoppers, four thrips, a number of scale-insects, four or five cicadae, etc., etc.¹

Most formidable in destructive power, and widest in geographical range is the "moth-borer," *Diatraea saccharalis*

¹ Kobus (1).

Fab. This form, or one closely allied to it, is met with wherever the sugar cane is grown. It is not very easy to give an idea of the injury caused by this caterpillar, which bores its way in all directions in the juicy cane-stalks. In one field, examined by the author in St. Kitts, five-sixths of the crop was destroyed by the *Diatraea*,¹ whereas the total destruction of crops is not unknown.² Its numbers may be gauged from the following figures. On the Brangkal Estate in Modjokerto in Java, 300,000 "borer" grubs were collected from the canes in the space of four months; and this does not appear to have been an exceptionally severe attack.³

The grub of a beetle, *Sphenophorus obscurus*, originally described as destroying the canes in the Sandwich Islands,⁴ has recently appeared in great force in Fiji. The whole damage during 1892 was estimated at 16 per cent. of the crop.⁵

Another beetle, *Apogonia destructor*, which commences its flights during the West Monsoon,⁶ does great damage in Java to the roots of the cane plant. Great care is taken in some estates to collect and destroy the mature beetles before the laying of their eggs. In February, 1896, twenty-three million were brought in by the collectors in ten estates; while in March of the same year, seventy-three million were destroyed in twenty-one estates.⁷

The direct effect of these insect attacks is various. In many instances the damage is temporary and the plant survives. In others the vegetative apex or the roots are destroyed and the shoot dries up. In the great majority of cases, however, the injury is probably an indirect one. The wounds made—especially by the stem-borers—serve as a suitable nidus for semi-saprophytic or parasitic fungi which are not able to penetrate the massive cuticle.

7. This apparent liability of the sugar-cane to the attacks of parasitic fungi and insects is not at all surprising. Whenever plants are cultivated on a large scale, diseases.

¹ Barber (1), p. 79.

² Cockerell (1).

³ Hein (1).

⁴ *Insect Life*, i., 185, 1888.

⁵ *Sugar Journal*, p. 183, 1895.

⁶ Zehntner (1).

⁷ *Archief*, 1896, p. 465.

sooner or later make their appearance. Forms which have been regarded as harmless suddenly assume dangerous parasitism, or those which have hitherto attacked other plants extend their destructive sphere—e.g., *Botrytis cinerea* and the vine. The conditions of cultivated plants render them peculiarly liable to the attacks of enemies. They are grown in large numbers, close together, so that the spread of disease is unchecked. Certain characters are developed in such plants by human selection: such are the great increase in size of parts (turnip root), the increased parenchymatosis of organs (cauliflower), and the accumulation of substances in the cell sap (beetroot, sugar-cane). All of these tend to disturb the equilibrium of a healthy condition. On the other hand, the selection of disease-resisting varieties is not prosecuted until a specific disease arises. It is not surprising then that, when diseases appear, they assume the greatest virulence, and frequently large areas are destroyed in a very small space of time.

The sugar-cane has peculiarities of growth and substance which render it specially liable to such attacks. Instead of the dry stem and soft leaves of most herbaceous plants, it has a juicy stem and tough, dry leaves. Gnawing and burrowing animals eagerly penetrate the hard rind; and free passage is thus offered for the spores of fungi. The mode of propagation of the sugar-cane is vegetative, by the rough and ready method of cutting pieces off the parent shoot; and by this means disease may be readily transmitted. There is no cessation of growth, as in colder climates, where many diseases are thus annually reduced. The plants are grown so close together that no other herb can exist in the fields when the canes have reached a certain age. The sugar-cane has been cultivated for thousands of years: it is not likely that the prevalence of disease is a new phenomenon in the fields; and, as we shall presently see, this is by no means the case. While singularly open to the attacks of parasites, the sugar-cane has great reproductive power. The plant body is divided into joints, each of which is provided with a resting bud, and each bud or eye may develop into a new plant upon

the ruins of the rotting cane. The success or failure of the growing and grown plant appears to depend less on the thickness of its skin, than on the vitality of the parenchymatous sugar-cells of its stem—whether or not they are able to resist the inroads of parasitic fungi when freely exposed to them.

8. The literature of cane diseases is of comparatively recent date, and this literature is probably due as much to the contest with beet as to any marked increase of disease during late years.

We have, unfortunately for our self-esteem, to look to a foreign country, where a little-known language is spoken, for the bulk of the descriptive work of the last ten years—and there was little done in the cane-fields before that time. It has been the enlightened policy of the Dutch planters to attach biologists as well as chemists to their three sugar stations in Java. And, thanks to the well-directed efforts of these investigators, we are to-day in possession of a valuable descriptive literature, which will serve as a basis for the study of sugar-cane diseases.¹

The Mid-Java Experimental Station has, it is true, ceased to exist; but a series of important papers were published there by Benecke, who also induced Möbius, Migula, Wieler, and other European botanists of note to contribute essays on special subjects for his journal.²

From the East-Java Sugar Station a series of papers have been issued by Valeton, Kobus, Wakker and Zehntner.³ Of the seventy odd pamphlets published at this centre, over one-third are devoted to diseases of cane plants.

We are indebted to the West-Java Station in Kagok-Tegal for papers by van Breda de Haan, Krüger and Went,⁴ describing a great number of parasitic fungi, while the late talented artist, Lucassen, has produced some excellent coloured plates of diseased canes.⁵

Not content with establishing these experimental sugar-

¹ Translations of many of these papers are published in *The Sugar-Cane* and abstracts are to be found in *Zeitschrift der Pflanzenkrankheiten*.

² Meded. Mid-Java.

³ Meded. Oost-Java, and later, *Archief*.

⁴ Meded. West-Java, and later, *Archief*.

⁵ Lucassen (1)

stations, the assembled planters of Java, in 1893, decided to establish a special journal devoted to cane matters, and placed the venture under the able editorship of Dr. Kobus, assisted by a strong editorial committee. The success of the scheme has been phenomenal. In the *Archief voor de Java Suikerindustrie*, as it is called, a series of valuable scientific papers have appeared in rapid succession. The journal has become the official organ of the sugar-stations, and all their publications are now first printed in its pages. The *Archief* forms already a bulky and indispensable addition to our sugar-cane library, and has met with warm eulogies at the hands of the scientific men at the head of the European beet industry. The specially favourable conditions prevailing in Java, coupled with the undoubted energy of the planters, have placed this Dutch island at the head of cane-growing countries.

9. In the British Colonies, as a rule, no officers are specially told off for the study of the sugar-cane and its diseases, and this work has fallen to the lot of Government Analysts and the Directors of Botanical Gardens. The latter officers are saddled with heavy administrative work, and hardly any descriptive work in cane diseases has been produced in their establishments.

The Director of the Royal Gardens, Kew, has to a certain extent supplied this deficiency, and has invoked the aid of specialists, some valuable papers by Michael,¹ Blandford² and Massee³ being the result. In these cases, however, the character of the work has suffered from its having been carried on in England; and many points have been left to be cleared up in the Colonies.

In the Australian Colonies there are government plant pathologists; and a careful study of cane disease has been made from time to time. Among these a specially able summary has been written by the pathologist of New South Wales.⁴

In the absence of leisure for special study, the great mass of the work done in the remaining British Colonies

¹ Michael (1).

² Blandford (1).

³ Massee (1).

⁴ Cobb (1).

has been the careful description of the symptoms on the spot and the forwarding of specimens of diseased canes to specialists in the United States and Great Britain for scientific description. Many of these parcels of diseased canes have been examined and reported on at Kew, and some of the reports have been published for general information.¹ Barbados, Trinidad, Antigua, St. Kitts, Demerara, St. Vincent, Jamaica and Mauritius have all been examined with reference to cane diseases; and in the bulky mass of official reports we have a tolerable enumeration of the more important pests in the Colonies.²

As regards British India, a good deal of information of a general character has been collected in the Dictionary of Economic Products.³

In this brief survey of the literature of cane diseases, the United States Experimental Stations must not be omitted,⁴ although much of their work is inapplicable to tropical countries, because of the presence of a cold season. It is especially noteworthy that the parasitic fungi do not seem to affect the Louisiana canes in any marked degree; while the various "borers" may be kept in check by special treatment of the plants during winter—a condition of things widely different from the never-ceasing circle of life and growth in the Tropics.

Lastly, the French Colonies, Martinique, Guadeloupe, Reunion and New Caledonia have not added much of value to the elucidation of disease phenomena; although specimens of canes have occasionally been sent to Paris, and examined and reported on by plant pathologists.⁵

10. One of the most puzzling features in the study of cane diseases is the concurrent presence of different parasites in the canes. It is frequently a very difficult matter to determine the real cause of any disease; and it is not surprising to find that the opinions of specialists are frequently

¹ See *Kew Bulletin*.

² See especially the Publications of the Botanical Departments and Experimental Stations of these Colonies.

³ Watt (1).

⁴ See especially the Bulletins of the Louisiana Sugar Experimental Station.

⁵ Prillieux and Delacroix (1).

at variance. To give an example of this, Went has lately described two very distinct cane diseases in Java. One of these he calls the "pine-apple disease," because of the smell of the canes attacked; and he ascribes it to the presence of a fungus which he has named *Thielaviopsis ethacetica*.¹ The other, which he terms "Het Rood Snot," he traces to a totally distinct fungus, *Colletotrichum falcatum*.² Massee, examining specimens of diseased canes sent from Barbados and St. Vincent, and experimenting with sugar-cane plants growing in Kew Gardens, has described a parasitic fungus *Trichosphaeria Sacchari* as the cause of the existing West Indian cane disease called the "rind fungus".³ He further concludes that *Thielaviopsis ethacetica*⁴ and *Colletotrichum falcatum*⁵ of Went are merely stages in the complicated life-history of *Trichosphaeria Sacchari*. Went in turn points out that *Trichosphaeria Sacchari*, although probably present in Java, is not at all injurious to the canes there and is merely saprophytic on dead canes. He further disagrees with Massee's conclusions as regards the relationship of these fungi, and lays stress upon the perfectly distinct disease symptoms of *Thielaviopsis* and *Colletotrichum* in Java and *Trichosphaeria* in the West Indies.⁶

The many papers during the last ten years dealing with "Sereh" furnish us with another case in point. This disease has been attributed by different authors to the most various circumstances. Worn out lands, unfavourable seasons, deep planting, artificial manure, root worms, parasitic fungi, bacteria and many other causes have been cited. Treub⁷ and Soltwedel⁸ regard it as a root disease due to Nematodes. Valeton,⁹ Krüger¹⁰ and Janse¹¹ on the other hand regarded the red-coloured fibrovascular bundles as the seat of disease, and the latter especially endeavoured to prove that bacteria played the same rôle in sereh as they do in "gumming".¹² Benecke¹³ strenuously opposed this view and called to his aid various European specialists,

¹ Went (3).² *Ibid.* (4).³ Massee (1).⁴ *Ibid.* (2).⁵ *Ibid.* (3).⁶ Went (5) and (6).⁷ Treub (1).⁸ Soltwedel (1).⁹ Valeton (1).¹⁰ Krüger (2).¹¹ Janse (1).¹² *Ibid.* (2).¹³ Meded. Ost.-Java.

including Migula.¹ Went,² in a bulky paper, has reopened the whole question. According to him sereh is caused by the combined presence of a leafsheath disease due to a fungus, *Hypocrea (Verticillium) Sacchari*, and a root-disease, bacteria also being incidentally present. It is known that bacteria, which are the cause of so many animal diseases, are not infrequently present in enormous quantities in plant cells without seriously affecting the life of the tissues; and comparatively few diseases in plants can be traced to their action. It is all the more necessary therefore to exercise caution in attributing any disease among plants to their sole agency. An almost exactly similar controversy has recently been raging concerning imputed bacterial diseases of the vine.³

11. The great mass of literature so briefly referred to is of quite recent date. This may be due to the gradual extension to the Tropics of the recent biological activity in Europe. As it becomes more difficult to find subjects for investigation in temperate climates, the overwhelming richness of tropical life in subjects of interest is gradually forced upon one. The earlier observers were unacquainted with parasitic fungi, and their works deal mainly with the insect enemies of the cane.⁴ On the other hand, the presence of trained botanists in the Java Experimental Sugar Stations has resulted in the description of numerous parasitic fungi not recorded elsewhere. Not only have the most destructive forms been carefully studied, but numerous less important discolorations of stems and leaves have been traced to the presence of hyphæ in the tissues.⁵ There is not the least doubt that many of these diseases, or corresponding ones, are present in every sugar-growing country.

A good deal of attention has always been paid to the insect pests in the Java cane-fields, and a zoologist is specially attached to the East Java Experimental Station. We have, therefore, a long series of papers on insects

¹ Migula (1).

² Went (1).

³ Prillieux and Delacroix (2). Mangin (1). Schilberszky (1), etc.

⁴ Guilding (1); Westwood (1); Roth (1), etc.

⁵ Wakker and Went (1).

attacking the canes.¹ In studying these insects, many of them are found to be severely checked by parasites. As an example let us consider the "moth-borer". Two species of minute egg-destroying *Hymenoptera* have been described from Java—*Chaetosticha nana* and *Ceraphron beneficiens*.² Attention had previously been drawn to the fact that, in the West Indies, but for the presence of a minute undescribed species of *Trichogamma* (?) destroying the moth-borers' eggs, it would be next to impossible to grow the sugar-cane.³ A species of *Mikrogaster* and a *Chalcid* assist in keeping down the moth-borer in New South Wales, attacking respectively the living caterpillar and the pupa.⁴ Lastly, a fungus, recently described as *Isaria Barberi*,⁵ has been met with attacking the caterpillars of *Diatraea Saccharalis* in the West Indies; and a similar form of "vegetable caterpillar" has been noted in Java.⁶

Wherever diligent search is made plenty of new species are forthcoming; and it is probable that additional forms of disease will be described when the cane-fields of Fiji, Cuba and the Sandwich Islands are more carefully studied. The history of the first observation of the "shot-borer," *xyleborus perforans*,⁷ and the "rind fungus," *Trichosphaeria Sacchari*,⁸ in the West Indies favours this assumption, in that when once attention was drawn to these diseases they were speedily found to exist over wide areas.

12. In view of these wide-spread disease phenomena it has been asserted that the cane industry is in danger of being wiped out from natural causes, independently of the beet competition; and that disease is much more prevalent than ever before. Certainly the stricken canes are visible enough. But it may well be that, in the former days of good prices, the planter could with equanimity leave the loads of rotten and rat-eaten canes upon the fields, while he cannot afford to lose a single cane to-day. We read that the sugar crop in Antigua was 3382 hogsheads in 1779,

¹ See especially papers by Kobus and Zehntner. ² Zehntner (2).

³ Barber (1), p. 148.

⁴ Oliff or Roebela, N.S.W. Appyelt.

⁵ Giard (1).

⁶ Kobus (1).

⁷ Blandford (1).

⁸ *Kew Bulletin*, March, 1894.

and 15,102 hogsheads in 1872; while owing to severe droughts in 1770, 1773 and 1778 there were no crops of any kind, and the whole body of negroes were in danger of perishing.¹

The records of the condition of the cane-fields in the past are very fragmentary. When the sugar-planters were in great prosperity, the remembrance of individual years of failure was quickly obliterated by succeeding plenty. Nevertheless we do read of severe epidemics among the canes: and the majority of these appear to have been much worse than any at the present time. A few instances will suffice:—

It is recorded by Patrick Browne² in 1756 of the "*Aphis blight*" that it was "generally pernicious to all plants on which it breeds: it has been some years known to destroy whole fields, nay whole crops of canes. When they are very numerous, people are obliged to burn everything about them, even the most promising plants."

In 1760 enormous numbers of "*Sugar ants*" (*Formica omnivora*) infested the cane-fields in the French and English West Indies. These caused such devastation that it was deliberated whether Barbados, formerly so flourishing, should not be abandoned. In 1876 the Government of Martinique offered a million of their currency for a remedy against the plague, and the Legislature of Grenada offered £20,000 for the same object."³

In 1771, Samuel Martin⁴ wrote concerning the "*Blast*" that it was "probable that the island of Antigua would in time be ruined by this disease". This latter appears to be similar to the *Aphis* of Patrick Browne. It is occasionally found in Antigua to this day.

In 1814, Lunan⁵ complained of the "*Blast*" in Jamaica "which often destroys whole fields of canes, and is caused by myriads of an invisible insect for which no effectual remedy has been found."

The Mauritius planters were greatly alarmed in 1848 because of the appearance in the fields of enormous

¹ Edwards (1), p. 447.

² Browne (1); Morris (1).

³ Schomburgk (1), p. 643.

⁴ Martin.

⁵ Lunan (1).

quantities of grubs which tunnelled into the heart of the canes.¹

We read that the introduction of the Bourbon Cane into India was followed in 1857-8 by such severe diseases that the canes were literally eaten out of the ground; and this valuable variety disappeared altogether from cultivation.²

During the same years in Louisiana a similar infestation of grubs appeared which caused great destruction on the Lower Mississippi. The canes broke to pieces in the fields and no reaping was possible.³

In the years following 1872 a terrible outbreak of rust appeared in Queensland and practically swept the cane-fields bare.⁴ About the same time we read of great epidemics in the Malay Archipelago, Mauritius, the Society Islands and Bahia.⁵

13. In attempting to form a conclusion as to relative abundance of present and past cane diseases, we are thus confronted by many difficulties. Our records of the past are exceedingly incomplete: increased scientific activity has of late years brought to light numbers of new parasites in the cane-fields: in these evil days the planter cannot bear the loss of the hundreds of rotten canes which so regularly litter the fields during the crop, and he becomes clamorous: we are still in ignorance of the causes of many diseases in the canes, and scientific opinion is not unanimous as regards those most studied.

There are many reasons for thinking that the assumed increase in disease during late years is more imagined than real. Taking a general survey, the cane-fields of the world appear to be fairly normal. Java, with all its diseases, seems to have them well in hand. It is principally in our own West Indian possessions, where scientific work is largely discredited, that the wave of disease is rising which threatens to carry away the last survivors in the economic struggle with the beet producers.

14. Our knowledge of the biology of the cane-fields has made rapid strides during recent years, and we are better

¹ Bojer (1); Westwood (1).

² Watts (1).

³ Cockerell (1).

⁴ Spon's Encyclopedia.

⁵ *Kew Reports*, 1877-8.

able to distinguish the work of different parasites than in the days of the "Blast". It does not seem, with all their variety, that the diseases are more fatal nowadays. In this, and in other respects, the cane epidemics of former days remind one of the "plagues" of the Middle Ages. The list of diseases to which the human frame is liable has been vastly lengthened by the advance of medical science; but the means of fighting them has increased in a much greater degree. The net result is healthier lives: may it be so in the cane-fields too!

It has been said that a healthy human stomach is cholera-proof: and a parallel may again be drawn with healthy cane plants. A cursory examination of the latter is sufficient to convince one that most, if not all, the diseases of past years are present in a subdued form. The Aphis of the "Blast," the "Sugar-Ant" of Barbados, the "Blackblight" and Cuckoospit, even the dreaded "Rust" of Queensland are all at the present moment widely distributed in the cane-fields, but not injuriously so.

On the other hand, just as new and obscure maladies appear at intervals among human beings, there are evidences of incipient parasitism among the cane pests. Saprophytic forms appear to have become parasitic, and feeble parasites have been changed into dangerous and destructive pests. The "Rind-fungus" of the West Indies appears to afford an example of this. *Trichosphaeria Sacchari* is regarded as an undoubted and dangerous parasite in these islands.¹ Although usually requiring a "bore-hole" for its starting point, evidence from Barbados appears to denote that this is not always necessary; for, as crop proceeds, an increasing number of diseased plants are met with which, after the most careful search, reveal no traces of borers.² In Queensland the *Trichosphaeria* has been proved by inoculation experiments to be an undoubted parasite,³ although it is far more abundant as a saprophyte upon the dead pieces of stems and leaves. In Mauritius it is doubtful whether the fungus is parasitic, although fairly

¹ Massee, etc. ² Barbados Experimental Station Reports. ³ Cobb (3).

abundant.¹ In Java, lastly, repeated inoculations have failed to produce any effect, and this fungus is therefore to be regarded as purely saprophytic.² There seems to be evidence that this form, belonging, as it does, to a saprophytic alliance, is acquiring parasitism.

It has been advanced that the altered behaviour of the fungus in various parts of the world is due to the different varieties of cane grown there. The determination and formation of resistant varieties is being prosecuted with vigour in many parts of the tropics. The rind-fungus appears to be only parasitic upon the soft, juicy canes of the Bourbon type. The "hard" *Caledonian Queen* and *White Transparent* varieties, even in Antigua, where the *Trichosphaeria* is rampant, are usually successful in resisting it.³ But the parasite appears to be gaining power. In a certain area in St. Kitts, in which island the Caledonian Queen has been largely grown for nearly twenty years, this hardy cane is already severely attacked;⁴ while one of the "hardy" varieties is reported to have been cleared out of parts of Martinique by the same disease.⁵

15. Of a similar nature to this incipient parasitism is the occasional change of habit in insects which may cause much destruction in the crops. This may be the case with respect to a small beetle *Xyleborus perforans* which has appeared in incredible numbers in West Indian canes during recent years. The case is interesting because this form was previously described as destroying wine casks, and the change from dry wood to juicy rotting cane is an extreme one.⁶

There appears to be no doubt that such a change of food has been observed in a minute *Tomicine* beetle found in Nevis.⁷ This species has been described as *Hypothenemus eruditus*, from its first discovery in the binding of a printed volume, and it has since been found in various dry substances. In Nevis, however, for a short time, its

¹ Boname (1).

² Went (5).

³ This has been frequently noted; see especially Watts (1).

⁴ Barber (2), p. 150.

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⁶ Blandford (1).

⁷ Barber (3) p. 122.

habits completely changed, and it burrowed into the youngest enrolled leaves of the cane shoot, causing a considerable amount of destruction. The case is remarkable in that beetles of this class do not attack the green tissues of plants.¹

Sereh is known to have existed in Java for years before it assumed its epidemic character.² The rind fungus is generally believed, in the West Indies, to have lived saprophytically on the cane for years before it acquired strength to attack the living cell; and the shot-borer probably lived in the decaying stumps of the tropical forest for many years before its food demands drove it to attack the canes. There are, so to speak, a host of lurking enemies ever ready to assume the offensive if by any means the cane becomes weakened.

16. With these facts before us, we seem to catch a momentary glimpse of a *grand rotation of disease phenomena*. The cane plants are constantly guarding themselves against the parasites attacking them; and many of the former pests, although present in the fields, have lost their parasitic power. Saprophytic forms as constantly acquire power to pass from the dead tissues and attack the living cells beyond; while those already feebly parasitic gain in power till they threaten to sweep all before them. From the few surviving canes again arises a more resistant variety, in its turn to fall a prey to new forms of disease—and so the cycle proceeds.

We may be encouraged if we can adopt this view. The inroads of the present-day pests will, in due course, be checked by natural means, even if the researches of scientific men fail to shield the planters from present ruin.

It is also encouraging to note that the patient application of scientific knowledge is producing results in fighting these diseases. While the West Indian planter has been too often content to fold his hands in resignation or despair, the Java cane growers are reaping the benefit of their more enlightened policy. The cane diseases are

¹ Blandford (2) p. 214.

² May (1).

accurately studied, and their causes, where possible, determined. Regular warnings are issued and special laws are passed: and thus alone is it that so terrible a disease as Sereh, although not stamped out, is restricted within reasonable bounds.

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Meded. W. Java, etc. = Mededeelingen van het Proefstation voor Suikerriet in West Java, etc.

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C. A. BARBER.

"WIND-SCORPIONS," A BRIEF ACCOUNT OF THE GALEODIDÆ.

THE name 'Wind-scorpion' is translated from the Arabic. It is applied to a little known but very important group of Arachnids, some genera of which contain individuals that reach a great size, measuring over two inches in length of body. The principal genus (*Galeodes*), which is that best known to the Arabs, is long-legged, very hairy, and so swift of movement that almost every writer who has had personal experience of these Arachnids has recorded his astonishment at the rapidity with which they cover the ground. A writer, in a private letter to Mr. Pocock, says that they look like a piece of thistle-down driven before the wind. There are, however, also short-legged genera, the members of which, although not so rapid, are yet reported to be extremely agile. In one genus the hind legs are said to be specialised for springing.

Pallas was the first European naturalist who recognised the animal as an Arachnid. Apparently on account of its long legs, he thought it was related to the Harvest-men, and called it *Phalangium araneoides*, or the spider-like Phalangium. Its general resemblance to a spider can also be traced in the German names "Scorpion-spinne," "Giftkanker" (= poison-spider), and even in the more modern "Walzen-spinne". It was Olivier who constituted it a new genus under the name of "*Galeodes*" (1791, *Encyc. Méthodique*)—a name perhaps referring to the helmet-like plate at the front end of the body. This plate is of such great morphological importance that it is well that it should be emphasised in the name of this group; for though traceable in most Arachnids, it is so conspicuous in the Galeodidæ as to distinguish them from all the other families.

The Galeodidæ do not make webs like the spiders, but hunt their prey in the open, fairly running it down. They feed chiefly on insects, moths, and even hard beetles, and will strike at almost anything that comes in their way,

scorpions, lizards, small mammals and birds. In one region their chief food is said to be the scorpions. A small nocturnal genus in Colorado is reported to hunt bed-bugs. The name given to the order, Solifugæ, refers to the habit of many genera of only appearing at night. Travellers in Asia, for instance, only see them in their tents, racing over their beds after dark has set in. Other genera, however, show no such aversion to daylight. In Santiago they are even said to run about the streets in broad daylight. It is well for the inhabitants that they are measured in millimetres and not in feet or even inches, for anything more terrible than the jaws of these creatures could hardly be imagined.

These formidable and conspicuous limbs consist of a pair of stout pincers arranged side by side, projecting straight out in front of the animal, with sharp, curved points, and toothed in various ways along the inner edges, the whole outer and distal surface of the limb being thickly covered by bristles. One writer speaks of them as the most horrible jaws in the whole animal kingdom, eclipsing even those of the tiger, the crocodile and the shark.

The method of using these weapons has been described as follows: seizing its prey the animal holds tight with one jaw, while it drives the other deeper in, and then holds tight with this one while the former is driven still further in, the two working alternately in a sort of sawing motion cut deeper and deeper into the victim, which is said often to be "completely devoured". This reported complete devouring of the prey is one of the many points that require investigation. It is worth comparing with the fact that spiders leave very little of their victims. The difficulty lies in the fact that the Arachnids, as a rule, take in no solid food at all, merely biting into the victim and then sucking all the juices out of the wound, these being well strained before entering the œsophagus. It has been suggested for the spiders that, in the act of biting, glandular secretions may cause the firmer tissues of their prey, which otherwise could not be sucked in, to deliquesce. Somewhat the same may be true for Galeodes.

Reaching out in front of the jaws, are the next pair of stout, jointed limbs which are remarkable for their length. These wave in the air as if to "interrogate space". They carry a remarkable and highly developed "smelling" organ, contained in an invagination at their tips. This organ can be protruded and withdrawn, and has given rise to some controversy. In Lichtenstein's description¹ the keen sense of smell of these hunters was rightly localised here, *i.e.*, in the swollen knob-like ends of these limbs. This view prevailed until Dufour, who seems first to have noticed the protrusion of the sense organs themselves, claimed them as suckers for holding prey. Other more recent observers who have watched the animal climb out of glasses, etc., touching the glass with the tips of these same limbs, have adopted Dufour's suggestion that they must be suckers to help in climbing. Another observer of the living animal, who was not aware of the presence of any protrusible organ, described the limbs as emitting a phosphorescent flame from their tips on being applied to any object. This appearance is quite explained by the glistening satin-like appearance of the chitin of the organ observable in its protruded condition. After all, the earlier view was the right one.

The mouth of the Wind-scorpion is a very minute aperture at the tip of a beak, which projects from between the bases of the last-mentioned limbs, but is not visible until the jaws have been pulled apart and raised. This beak, which is quite rigid, is evidently forced by the penetrating action of the jaws into the wound. The juices which are sucked out, are strained through an elegant lattice-like sieve which stands out at the tip of the beak, and is constructed out of the fringing bristles. So finely does this sieve strain the food that on one occasion I found moth-scales retained on its outer surface while, here and there, in the intestines of the same animal, a few similar scales were found, evidently sucked in by the strong pumping of the œsophagus, but in each case apparently forming a centre of disturbance to the normal processes of digestion.

¹ Lichtenstein and Herbst, *Naturl. Insecten, Gattungen Solpuga und Phalangium*, Berlin, 1797.

Another question which requires to be established experimentally is the amount of truth there is in the evil reputation which these Arachnids have for inflicting very painful and even dangerous bites. Lichtenstein (*l.c.*) has endeavoured to show that certain passages found in the ancient classics refer to Galeodes. The "mice" which plagued the Philistines (1 Sam. v. vi.) when they captured and kept the "ark of the covenant" must, according to this writer, have been the terrible Galeodes, while the "emerods" with which they were also plagued referred to the sores caused by the bites of these animals, chiefly on the pudenda. Among other arguments in support of this interesting interpretation of the ancient Hebrew story the same author asserts that Galeodes still inflict similar bites either in the same place, especially of females, or on the lips of people or animals sleeping on the ground. Again, a long passage is quoted from Agatharchides to the effect that a populous district on the shores of the Indian ocean was deserted owing to the swarms of these Arachnids that appeared after a very long rainy season.

On the other hand, Olivier disbelieved the awful reports of the Arabs, who were terrified at the sight of the Galeodes which appeared in the tents at night, and who told yarns, each more horrible than the last, as to their dangerous bites. He admitted however that if the animals did bite, with *such* jaws the results would probably be painful. Pallas says that people are bitten "accidentally" by the animals getting under their clothes and relates a few such cases. Dufour also records a case of a man in Algeria being bitten by a Galeodes that got under his clothes. The descriptions given by these two authors of the effects of the bites, the accuracy of which there is no reason to doubt, are enough to account for the exaggerated terror with which these animals are commonly regarded by the natives in the countries where they occur. This is probably the correct view of the case, and is quite in accord, on the one hand, with the statement that the animals are perfectly harmless, and, on the other, with the description of their ferocity when molested.

Before leaving the subject of the results of the bite, it is to be noted that all the early writers assume it to be extremely poisonous; compare, for instance, the German name for *Galeodes*, "Gift-kanker". Further, the pain and violent inflammation caused can hardly be accounted for except on this assumption. Dufour searched in vain for poison glands such as those well known in the jaws of spiders, and not finding them gave the problem up. The present writer has suggested that the poison may be the result of simple exudation of matter through the setal pores which can be traced along the tips of the pincers. Such matter would be partly excretory, and hence deleterious to living tissues. It would probably be closely allied to that which, in the hypodermal cells, builds up the chitin and supplies material for the bristles. On the other hand, Captain Hutton records¹ the case of a lizard bitten by a *Galeodes*, which entirely recovered in three days, and uses this as an argument against there being any venom transmitted by the bite. Here the matter rests for the present; we know little beyond the facts that there are no poison glands and that the bite nevertheless sets up violent inflammation.

Among other points to be investigated, mention should be made of the marvellous variety of bristles and hairs which cover many parts of the body; the forms and uses of these are well worthy of study. One obvious suggestion is that they are to a large extent protective. After a good meal, the bag-like abdomen of *Galeodes* may be stretched by fluids to such dimensions that the animal can hardly crawl away. At such a time it would form a rich and easily digested nitrogenous morsel for birds and small mammals. One of its characteristic attitudes of defence is to raise its abdomen right over its back, so that that defenceless member may come under the protection of the legs, for it is on the limbs that the most marvellous bristles occur. Among them are certain curious forked hairs which I have suggested may act as buttoned rapiers, safe to the animal itself but

¹ *Ann. and Mag. Nat. Hist.* vol. xii., p. 81, 1843.

dangerous to any larger creature which, snapping it up, might break off the forked end of the bristle and receive a possibly poisonous wound. On the other hand, birds have actually been seen¹ attacking Galeodes, although the observations are hardly sufficient to warrant any definite conclusion either way. Here again experiments are very desirable.

The claws of this formidable Arachnid also deserve mention; they are as terrible, in their way, as are the jaws. They are very long and curved, and their tips are movable. A tendon runs up the hollow of the claw and bends the tip, when needed, sharply round. This mechanism enables the claw to be firmly anchored in the body of the victim.

Galeodes stridulates when enraged, and possibly also at periods of sexual ripeness. While watching a specimen which, being confined, was in a "positively astounding fury," Pallas heard the screeching sound which the animal made by rubbing its jaws together. As far as I know, there is no record of any one else having heard this sound, but stridulating ridges have recently been discovered by Hensen and claimed as such by him, although he was apparently unaware that the sound produced by them had been heard by Pallas. These ridges do not occur in all species. Both Spiders and Scorpions are now known also to stridulate; the apparatus, however, seems to be different in each group. This somewhat remarkable fact tends to support the view of the present writer that these different Arachnids cannot in any way be deduced from one another, but are separate developments of some common ancestor.

A few of the more noticeable structural features may be briefly mentioned. The enormous jaws differ from those of all the other larger Arachnids in being hinged on to the front lateral edge of the exoskeleton. The hinge has been formed secondarily out of a crumpling and folding of the skin at the side, and is clearly an adaptation to the great size, and to the powerful muscles of these limbs. The chitinous infoldings forming these hinges give rise to the peculiar areas on each side of the "head," which have given

¹ Distant, *Nature*, vol. xlv. p. 247.

rise to much speculation. Their purely secondary origin is shown in the fact that the folds which mark them off have come between the large median eyes and the lateral eyes, quite displacing the latter.

With regard to the eyes, it was long thought that the Galeodidae differed from all the other large Arachnids in having no lateral eyes. But as long ago as 1826 lateral eyes were attributed to Galeodes by so great an observer as Johannes Müller.¹ He claimed six eyes, whereas no one else could find more than two. This claim seems generally to have been dismissed by students with astonishment. One pair of the extra four eyes, for instance, could be explained as the tubercular bases of the pair of bristles often found in front of the large eyes; these, with the bristles knocked off, might be mistaken for eyes. The other pair could not be found at all until quite recently, when, in working over sections, the present writer found two pairs of very degenerate lateral eyes in a species of Rhax, and afterwards discovered similar structures in other specimens. They were not found, however, till long after Johannes Müller's apparently utterly erroneous assertion that Galeodes had six eyes had been dismissed and completely forgotten. Having again looked up the original, the present writer has no doubt that the lateral eyes which he thought he was the first to discover had already been noticed and their true nature guessed seventy years ago. They so little resemble eyes, and the position into which they have been forced by the formation of the hinges for the jaws is so unlikely a place for eyes, that there is little wonder that, until the retinæ were actually seen in sections, they were never again recognised.

Upon the last pair of legs occur the "raquet organs" which have also greatly puzzled naturalists. These are fan-shaped structures supported on short stalks, five on each leg. They are purely sensory, and appear to be erectile. The nerve-endings open round their distal edges. The earlier writers justly compared them with the combs

¹ Vergleichende Physiologie des Lichtsinnes.

of the scorpion, although they should more correctly be compared with the teeth of these combs. Both appear to be functionally connected with the reproductive processes, occurring as they do in *Galeodes* just in front of, and in *Scorpio* just behind, the genital aperture.

So little indeed do we know of these animals that there is still no agreement as to the characters of the sexes. How little reliance can be placed upon the earlier records which speak of male and female specimens may be gathered from the fact that until quite recently the large fusiform spermatophores, which often completely fill the genital glands and may even be visible through the skin of spirit specimens, were generally assumed to be eggs. I have seen many specimens with their glands filled with these white glistening spermatophores, and am still uncertain whether they are males waiting to discharge them or females which have received them. It is quite probable that the females receive many more spermatophores than they require. The superfluous ones are said to be devoured by amœboid corpuscles which also dispose of the spermatophoral envelopes [Birula].

The female is said to attack and devour the male as soon as she has received the spermatophores. This conjugal ferocity is, however, somewhat compensated for by maternal tenderness. The females have been watched digging holes in the ground in which the eggs are laid, the eggs being probably stuck together and protected, as in *Thelyphonus*, by a glutinous secretion.¹ The hatched-out young are closely guarded and watched by the mother. The earlier developmental processes themselves are still quite unknown.

How much we yet have to find out about these formidable yet fascinating Arachnids can be gathered from these

¹ This would, doubtless, be comparable with that which sticks the eggs of the Book-scorpions to the abdomen of the parent, and, further, with that which in *Phrynus* forms the cocoon. This coarsely woven cocoon of *Phrynus* leads on to the web-spinning of the Spiders, so that the elaborate nets of these latter for catching prey can be traced back step by step within the Arachnid phylum to the simple beginning still found in *Thelyphonus* and probably in *Galeodes* of protecting the eggs with a glutinous secretion.

few brief notes. Every one who works at them deplors the scantiness of our knowledge. While the Spiders hang out their marvellous webs on every bush, and the Scorpion's sting is a household word, Galeodes has suffered for lack of sufficient advertisement. It is one of the objects of this paper to press home the claims of this family to the attention of naturalists. The collections, even in our largest museums, are very small, and reliable observations on the living animal are scanty in the extreme, and yet I think it will be admitted by my readers that these Arachnids rival both the Spiders and the Scorpions in interest.¹

But even if our knowledge of the various forms, and the habits of life of the Galeodidæ were far more complete than they are we should still not be satisfied. We can no longer stop at admiration and minute description of existing forms alone. It is now generally recognised that the most stationary of organisms are not really stationary, but are all plastic and variable. They change as the environment changes, responding with exquisite sensitiveness to any alteration in the impact of their material surroundings. Important, perhaps pre-eminent, amongst these varying factors must be reckoned the food supply. It is a firm conviction of the present writer that no other factor has played so large a part in bringing about the multitudinous forms of animal life as the acquirement of new methods of feeding. The bearing of this upon the origin of the Arachnida will be explained more in detail in what follows.

According to the modern view, the Scorpions with all their many though, comparatively speaking, slight variations (for the Scorpion ranks high among the more stationary forms, having varied but little from the type of its Silurian ancestors) represent so many plastic waves which have radiated out from some centre, changing as

¹ I should like to add that the death of a brilliant young American naturalist, J. Duncan Putnam, at the early age of twenty-six deprived this family of an enthusiastic advocate. Putnam, on his first acquaintance with them was fascinated by them, and began to investigate them systematically. Among other studies, he compiled a list of 224 treatises and references in the literature (up to 1881, the date of his death) dealing with these animals; of this number hardly 10 per cent. are original observations.

they went in adaptation to their changing circumstances. Similarly the Spiders, far surpassing the Scorpions in richness and variety of the present forms, have spread over the face of the earth as so many modifications of some ancestral spider. Further, comparison of the general structure of the Spiders and Scorpions shows that their ancestral forms were related, *i.e.*, were themselves variations of some still earlier Arachnid form which was neither a scorpion nor a spider, but yet gave rise to them both.

A new ideal thus ennobles the science of Zoology. Animal forms are no longer merely minutely described but analysed, and by a careful comparison of the different forms composing a group, the more fundamental features are sifted out from the more superficial variations until we are able to picture to ourselves with more or less accuracy a hypothetical ancestral form which could have given rise to all the existing members of that group.

In this way it ought at first sight to be possible theoretically to reconstruct with some degree of accuracy the form of the original Spider or Scorpion by selecting with care and judgment those characters which are common to all Spiders or Scorpions and which therefore appear to be their common heritage. As a matter of fact, however, the process is not so simple. We cannot hope to arrive at any true idea of the primitive Spider or Scorpion without all the while keeping the other Arachnid forms, the Book-scorpions, the Pedipalpi, the Galeodidæ and the Mites constantly in sight. A character, for instance, which is present in all Spiders may be so variable that it is not always possible now to determine what its primitive condition was without comparison with the homologous structure in the other Arachnids. I say not "always" possible, because there are adaptations which are so obvious that it is not difficult to decide which is the simpler and primitive and which the more complex and secondary. Practically, therefore, the method of analysing each group separately is not to be recommended. An attempted reconstruction of the primitive Spider requires constant comparison with the other Arachnids.

The two forms which have been most diligently studied in the past have been, as above noted, the Spiders and the Scorpions, with some reference to the large Pedipalpi. The Book-scorpions and the Mites, being smaller forms, have been left somewhat on one side, while the very important claims of the Galeodidæ to a voice in settling the family tree of the Arachnida, although long ago put forward, are only now beginning to be closely examined.

Here, then, is another inducement to collectors and naturalists, not only to make good the deficiencies in our museum collections but also to supply material to our laboratories; for the morphological interest centring in the Galeodidæ is as great, if not greater, than the biological.

I propose, then, as briefly as possible, to describe comparatively some of the special features of the Galeodidæ, in order to show how near they take us to a reconstruction of an ancestral form capable of producing all the known Arachnids.

In all segmented animals, no matter what theory we adopt as to the origin of metamerism, we are justified in assuming that that form which shows the segmented condition least modified and obscured by fusions and distortions of segments remains in this respect nearest the common ancestor of its class. Few animal groups show such a marvellous variety of modifications of the primitive segmentation as the Arachnids. Each family has its own distinct methods and degrees of fusion, and what is most remarkable is that these different fusions seem to be distinct from one another. This is very important because it appears unmistakably to prove, what we have already suggested above, that all the Arachnid families are distinct specialisations of some primitive form, *i.e.*, they cannot be deduced from one another.

These different fusions are worth noting and comparing. Galeodes has the first three segments fused and all the rest free; the sixth and seventh, however, are modified by the constriction between them being drawn in to form a waist. Behind the waist all the ten segments are swelled up to form a bag-like abdomen capable of enormous ex-

pansion. *Schizonotus*, which is a most remarkable but little known form, superficially resembling *Thelyphonus* but with a jointed cephalothorax and the large helmet-plate like *Galeodes*, appears to have the first four segments fused. *Scorpio* has the first six segments fused, and no external trace of any waist, although, internally, the constriction between the sixth and seventh segments has been drawn in to form a diaphragm; all the segments behind the seventh are free. Seven of these are swelled up to form a distensible bag, while the last five show an exactly opposite specialisation; they are thin, drawn out, thickly armoured and firmly hinged to one another to form an almost invulnerable tail, the terminal joint of which is armed with a sting. *Thelyphonus* has the first six segments fused rigidly together so as to form a long narrow cephalothorax, a waist between segments six and seven, nine abdominal segments free and forming a distensible bag, and three minute telescoped segments forming a sort of short tail which carries a long whip-like appendage. *Phrynus* differs from *Thelyphonus* in having the first six fused segments so compressed longitudinally that the cephalothorax is as broad or broader than it is long, while the tail segments are more telescoped and not furnished with any caudal appendage. The Spiders have the first six segments fused into a compact round or oval cephalothorax, a waist between the sixth and seventh segments, and all the abdominal segments fused together. These latter nevertheless form a distensible bag, but not by any means so distensible as in the case of the other Arachnids with freely telescoping abdominal segments. The Book-scorpions have the first five or six segments fused, no waist visible, all the abdominal segments free and forming a distensible bag. The other families, Harvestmen and Mites, departing somewhat far from the leading types here described, need not detain us.

Now, of these various fusions and specialisations of segments *Galeodes*, with only three fused segments, shows far and away the least modification of an assumed freely segmented ancestor. No other Arachnid (except *Schizonotus* and, perhaps, some of the Book-scorpions) has less than six,

while the Spiders have all the segments fused into two compact groups joined together by a waist.

On analysing and comparing these different fusions and modifications of segments, we find three features common to them all. In all at least the first three segments are fused together, and in all there is some trace of a waist between the sixth and seventh segments, and in all the segments immediately behind the waist are capable of distention. In these facts we may therefore find some indication as to what the common ancestral Arachnid was like.

Hitherto, discussions of affinities based upon segmentation have dealt almost entirely with the number of segments. Most of my own work with Arthropods has gone to show that, important as are the fusions of segments treated quantitatively, that is not enough. The segmentation must be studied and compared qualitatively. It is not enough to ascertain merely how many segments are incorporated in each fused area, we must also ascertain how they have been fused together, that is, how distorted in the process, and, where possible, why they were so modified. Some idea of the importance of this qualitative study of segments will be gathered in the following pages.

Now the fact that the Galeodidæ have, alone among Arachnids, retained the primitive number of fused segments, would lead us to expect that they would also show the qualitative nature of this fusion more clearly than any other Arachnid. And this is indeed the case. Careful examination of the relative character and position of the limbs and mouth, compared with what we know of the nature of the food, shows that this primitive fusion and distortion of the segments must have been brought about as an adaptation to a special manner of feeding. What this method of feeding is, we have already described: the first pair of limbs are thrown forward on each side of and above the anteriorly placed mouth; they seize and crush the prey, the blood of which is then sucked out.

If now we can further show that the ancestral Arachnid fed in the main as Galeodes feeds, we should then have

still further light upon the shape of this primitive form, for we should be justified in assuming that the exact method of distortion of the early undifferentiated segments was in the main that which still persists in *Galeodes*. As a matter of fact, then, we do know that the method of feeding of *Galeodes* was the primitive method. All the principal Arachnids still seize and crush their prey with either the first or the first and second limbs, which are thrown forward round the mouth, and the juices are sucked out. I say all the principal Arachnids, for in some of the more specialised groups, the Harvestmen, and the Mites, the type may here and there be departed from. But even in these forms it persists with sufficient frequency to justify us in concluding that this method of feeding was first acquired by the ancestral Arachnid from which all the existing derivative forms must have inherited it. So much indeed we could have arrived at without the assistance of the *Galeodidæ*, but it is doubtful whether we should ever have unravelled the actual mechanical distortion of the segments which led to the initial differentiation of the primitive Arachnid from its more simply annulate ancestors, but for the persistence of a form which has never added to the primitive number of fused segments.

What then was the nature of this primitive distortion of the three anterior segments, so far as we can gather it from the conditions found in *Galeodes*? Our analysis leads to the following conclusions:—

1. The segments were at one time simple annular segments like those along the rest of the body; the mouth opened on the anterior face of the first segment; a large fleshy prostomium or upper lip protruded anteriorly above the mouth; and from the side of each segment a pair of simple limbs, richly covered with bristles, projected laterally. That is this analysis takes us back to a simple Chaetopod Annelid.

2. This simple condition was first departed from by the bringing forward of the first pair of limbs to the sides of and slightly above the mouth. The two limbs, thus arranged side by side at the anterior end of the body, not

only squeezed and depressed the prostomium or upper lip between them but entirely altered the shape of the first segment to which they belonged. The sides of the segment on which they were originally inserted with the surrounding regions to which their muscles were attached must have shifted from their original positions and become the bases of the limbs in their new positions. The lateral regions of the first segment were thus gradually folded upwards over its dorsal surface. In time as the limbs grew in size and strength and required larger and deeper bases, these folds spread backwards over the dorsal surfaces of the second and part of the third segments, the two folds eventually meeting in the middle line, obliterating the old dorsal surface with the exception of one small island which carried the eyes. In all existing Arachnids the lateral folds of the first segment, carrying the first pair of limbs, have met along the middle line, the junction being still marked by a suture through which in many forms the ocular tubercle protrudes; but the fact that a fossil scorpion from the Silurian shows an irregular shaped island of the dorsal surface not yet covered over by these folds makes it doubtful whether they ever actually met in the ancestral form. The meeting may have been a later specialisation of the derived forms.

3. This translocation of the first pair of limbs to a position above the mouth made room for the second pair to come forward also. This they did, and took up positions at the sides of and slightly below the mouth, their coxal joints pointing forwards. In some cases (*e.g.*, *Thelyphonus*) they have fused longitudinally below the mouth just as the basal regions of the first pair fused together above the mouth.

4. The anteriorly placed mouth was thus in time surrounded by limbs, two above and two below, and its shape became specialised accordingly. The prostomium squeezed between the jaws fused along its lateral edges with the edges of the underlip which had been forced to protrude anteriorly by the forward movement of the limbs of the second segment. In this way a sort of rigid beak was

formed, with a small mouth aperture at its anterior end. This beak persists in the Galeodidæ. It is found also in the Book-scorpions, in some Mites, and, though it is here of no further use as a beak, in Thelyphonus. Further, the mouth parts of Scorpions, Spiders and of Phrynus can all be deduced from such a beak by the suppression and modification of different parts. There is thus an abundance of evidence that the mouth in the primitive Arachnid was at the end of a beak in all essentials like that still persisting in Galeodes.

Thus by the aid of the Galeodidæ, the initial distortion of the primitive segmentation which transformed a simple Chætopod into the ancestral Arachnid can be unravelled, while its physiological significance as an adaptation to a new method of feeding is clear. We have now to show how profoundly this initial adaptation modified the whole of the rest of the organisation of the ancestral form and consequently of its derivatives, the existing Arachnids. We must limit ourselves to a few of the more important structural features which can, with every probability, be shown to be concomitant adaptations.

The waist or diaphragm.—This constriction, which occurs, as we have seen, in all the larger Arachnids between the sixth and seventh segments, must be regarded as inherited from the primitive form. Its significance is not far to seek. The region anterior to the waist contains the central nervous system and the powerful musculature for moving the proximal joints of the limbs. Now not only does the pumping action of the œsophagus suck in the juices of the prey but, like a force-pump, it drives the liquid food into the alimentary system, distending it to its utmost capacity. This arrangement obviously requires regulating. Undue pressure on the nervous and muscular tissues has to be avoided. Hence we find a general tendency for the alimentary system to lose its lateral branches or cœca in the anterior region, and, compared with its condition in the distensible abdominal region, to be but feebly developed. On the other hand, behind the waist or diaphragm, the alimentary system is enormously developed, and complicated systems of branching diverticula, different

in the different Arachnids, fill up every available corner of the abdomen left free by the circulatory, respiratory and genital systems. Into this richly branched alimentary system the liquid food is pumped to its utmost capacity, and, owing to the diaphragm, without any danger of disturbing the nervous and locomotory systems of the anterior region. Further, there is some anatomical evidence to show that when the abdomen is distended with liquid food the alimentary canal can be constricted as it passes through the waist or diaphragm, as an extra safeguard to prevent the liquid food from flowing back into that portion of the alimentary system which runs through the anterior region.

The habit of distending the abdomen to monstrous proportions with liquid food seems common to all the larger Arachnids. Individual specimens with distended abdomens may of course be gravid females, but as often as not, they are animals which had been killed just after a full meal. The most familiar Arachnid thus distending itself does not, however, happen to be one of the large forms, but a Mite. I refer to the Ticks which, before fastening on to their hosts, are quite insignificant in size, but, when once fixed, suck in so much blood that they swell up to the size of a bean. It seems, indeed, as if their tough skins were as much an adaptation to prevent them from bursting through over-feeding, as to defy the efforts of their hosts to scratch or rub them off.

The Degeneration of the Abdominal Limbs.—The differentiation of the body into an anterior locomotory and a posterior vegetative region sharply divided from one another, has led to the degeneration of those limbs which originally belonged to the segments of the posterior region. We have every reason, however, to believe that, in the ancestral form, they long persisted in a more or less useless condition. A few of these aborting limbs have been utilised by the different existing Arachnids, but in very different ways. Those of the first abdominal segment generally persist as protections for the genital aperture, as a rule simplified to a pair of covering scales, but in Harvestmen and certain specimens of *Phrynus* they form distinct

appendages, for there is every reason to believe that the long genital process of the former is really derived from a pair of limbs. The limbs of the second segment persist only as scales covering the apertures of the tracheæ in Galeodes, but in Scorpio they are still more or less leg-like and are specialised as sensory appendages—the “combs”. Further, we have spinnerets, two pairs in the spiders. These are very large and jointed like legs in some forms. And lastly, we have the sting of Scorpio which is perhaps best accounted for as having been formed out of the limbs of the last segment, fused posteriorly over the anus. This would at least account for the *pair* of poison glands with two distinct ducts and apertures.

Specialisation of the Respiratory Invaginations.—An interesting problem is presented by the respiratory system of the ancestral Arachnid. What was it? We have at least three distinct types of respiratory cuticular invaginations in existing Arachnids. As the most highly specialised we have what are known as book-lungs, because the air runs in flat spaces separated by chitinous laminæ within which the blood circulates; these are arranged alternately like the leaves of a book. Such localised lungs necessitate a highly organised circulatory system. They are found in Scorpions, Pedipalps and Spiders. A second well-marked kind of respiratory invagination occurs in the Book-scorpions, Harvestmen and some Mites. It is a simple tubular invagination, the inner end of which widens and then breaks up into an enormous number of long fine tubules carrying air into the remotest parts of the body. These are called tuft-tracheæ. Lastly we have the ordinarily branching tracheal tubes which are best developed in the Galeodidæ.

These three forms of respiratory invaginations must certainly be regarded as modifications of some simpler form, from which they could all be derived. I say “must” because they all open in exactly the same association with limbs or limb-vestiges and are thus certainly homologous structures. There can, I think, be little doubt that these different forms of tracheæ are due to the different ways in which the alimentary canal has developed under the influence

of the force-pump action of the œsophagus, for the respiration is always intimately associated with the circulation, and it is this latter that would be affected first of all by any great extension of the alimentary system. This subject would, however, require more details for its elucidation than the limits of this article would permit. I have dealt with it in detail elsewhere.

The Number of Pairs of Stigmata.—Although, in existing Arachnida, the respiratory invaginations are now confined in each form to a very few segments (at the most four, Galeodes, Scorpio) we are fully justified in asserting that, in their simple condition in the ancestral form, they were present, one on each limb, throughout the whole extent of the body. Specialisation of this diffuse condition must very early have set in, indeed such limitation must have proceeded concurrently with the differentiation of the body into two regions. The restriction of the digestive and generative processes to the abdomen would tend to confine the circulatory and respiratory mechanisms also to this same region. Hence, we find the respiratory invaginations early disappearing from the anterior region. This disappearance would be still further accelerated by the tendency to knit the whole of the anterior region into a rigid skeletal box specialised purely for the mechanism of locomotion. It is strongly confirmatory of the whole line of argument here used that the only Arachnid (omitting the Mites) which has retained a pair of respiratory invaginations in the anterior region is also the only Arachnid which has never added any segments to the first three, the fusion of which, as we have above endeavoured to show was the initial specialisation which differentiated the class Arachnida from their Annelidan ancestors. In all other existing Arachnids, except in certain Mites, the respiratory invaginations have disappeared entirely from the anterior region.

Those on the abdomen on the other hand seem to have persisted for a long time as a complete series, although here also they early began to degenerate progressively from behind forward, so that they are now only found in a few pairs on the anterior abdominal segments close

behind the genital aperture. This progressive disappearance of posterior stigmata can still be followed in the Galeodidæ, where the whole aspect of the middle line of the abdomen suggests the disappearance of a long series. Three pairs are said to occur in the genus *Datames*.¹ In the genus *Galeodes*, the most posterior of these is degenerated to a single aperture, the tracheal tube to which appears to be aborting and in some cases seems actually closed; while in the genus *Rhax* this last pair has finally disappeared, leaving no trace either of aperture or tube. The reason for this degeneration of the posterior stigmata requires investigation.

In the Book-scorpions there are only two pairs functional with seven pairs of scars which I have claimed as the vestiges of stigmata. In *Thelyphonus*, behind the two functional stigmata, scars are found as far back as the eighth abdominal segment, these scars showing not only traces of the former stigmatic apertures but also of the hard convex scale-like plates to which the limbs associated with the invaginations had been reduced. These plates are very marked in *Scorpio* where they are still functional, and serve no doubt to protect the specialised lung from external pressure.

The Endoskeleton.—The remarkable endoskeleton which is a characteristic of the Arachnida, and differs in each form, has been the subject of a considerable amount of discussion. The clue to its right understanding has again been supplied by the Galeodidæ. We gather from the condition of the unfused abdominal segments in the Arachnida that originally, *i.e.*, in the ancestral form, all the harder rings of skin representing the segments were separated by very flexible intersegmental membranes. In the abdominal regions these are utilised in the formation of the collapsable vegetative sac. Between the sixth and seventh segments this membrane has been drawn in to form the waist or diaphragm, while in the region in front of the waist, on the harder rings fusing together to form a rigid cephalothorax, these

¹ According to a figure by Putnam.

membranes were drawn into the body to form an internal skeleton, the shape of which varies according to the ways in which the component segments have coalesced. A comparative study of these endoskeletal structures and the different ways the segments have been knit together shows this beyond dispute. In the Galeodidæ, in which the three posterior segments of the anterior region remain free, the endoskeleton is limited to one single pair of infoldings, *viz.*, of the membrane between the third and fourth rings. What is also important is that in Galeodes this endoskeleton is clearly seen to be nothing but an infolding of the exoskeleton, whereas this origin is now difficult to establish in the cases of the other Arachnids, specialisation having gone so far that the whole structure seems more like a complicated framework of sinewy or tendinous matter than a derivative of the chitinous cuticle by simple infolding. This structure, then, is clearly due to the differentiation of the body into two highly specialised regions.

These, then, are a few of the structural modifications early initiated in the ancestral Arachnid and due to the further specialisation of its adopted method of feeding. These again have been carried further in various directions by the different descendants of that ancestral form, the modern Arachnids. In nearly all cases, it will have been observed, the Galeodidæ have retained the ancestral conditions least changed.

Before summing up these points in order to obtain a rapid outline sketch of the ancestral form as here reconstructed, another point of importance claims our attention. The ancestral form must have been marvellously richly supplied with glands of some simple kind from which the many glands to be found in the Arachnida could be deduced. There are poison glands, glands for sticking the eggs together (cement glands), and glands, the sticky secretion of which, hardening as it is drawn out yields the silk for cocoons and webs, and, lastly, stink glands. That all these are derivatives of some common form of gland is evident to any one who makes a comparative study of them. The

web of the Spiders¹ for instance comes partly from glands which are serial with the cement glands of the Book-scorpions. These again are apparently homologous with the gland supplying the coarse silk for the cocoon of *Phrynus* and the glutinous matter sticking together the eggs of *Thelyphonus*. Again, the web-spinning glands of the Book-scorpions open at the tips of the jaws close to where, in the Spiders, the poison glands open; while the glands of the spinning Mite (*Tetranychus*) open in the corresponding place on the second limbs, and the poison glands of the Scorpion open at the tip of the sting which I regard as a pair of fused limbs (see above). Lastly, the poison glands of *Scorpio* are probably homologous with a pair of large glands in *Thelyphonus* said to emit an offensive and volatile fluid, only here the limbs have degenerated and the glands open one on each side of the anus.

Of the above-mentioned glands the Galeodidæ possess only one pair, and that of a very simple character. They open just within the genital aperture and probably yield a sticky secretion for the eggs; there are no poison glands, no spinning glands, no "stink" glands. This is important, for it indicates that none of these glands in their specialised forms were present in the ancestral Arachnid. Indeed, this is obvious from the fact that they do not appear in exactly the same place and character in any two existing Arachnids, whereas had they developed in the ancestral form, we should have found more uniformity in their distribution and character in its descendants. But the Galeodidæ, if they have no glands, are as we have noticed above, extremely rich in bristles and hairs, and this same character we may safely predicate of the ancestral form. We shall probably then not be far wrong if we trace back all these glands to the small cuticular sacs out of

¹ It is worth noting that the marvellous web-spinning of the Spiders, and secondarily also the peculiar form of their abdomens are, in all probability, due to the early fixing of their spinning-glands far back on the abdomen. This position, the movement being from the waist, gave the threads a longer throw.

the bases of which in the primitive and more soft-skinned ancestor the bristles grew. The material which originally formed a bristle may be supposed to have been retained in a modified and fluid form within the sac which, in its turn, grew larger and larger to form the highly specialised poison or spinning glands of the modern Arachnids. I feel sure that an exhaustive comparative study of the bristles and glands of the Arachnida would completely establish this.

Let us then briefly sum up the characters which we can safely attribute to the ancestral Arachnid as soon as the evidence of the Galeodidæ is added to and compared with that obtainable from the other Arachnids.

We must picture to ourselves a loosely segmented hairy creature showing a slight waist-like constriction between the sixth and seventh segments. The first three segments are fused together and distorted in such a way as to range two pairs of limbs round an anterior mouth which is at the tip of a kind of beak. These limbs are specialised for seizing prey and crushing it in front of the mouth. The four following pairs of limbs are used for locomotion, while those of the segments behind the waist which are often swelled up by liquid food are more or less useless and degenerating. This, in brief, would represent the form from which, by modification and specialisation in various directions, all the existing Arachnida could be derived.

Having now reconstructed an ancestral form for the Arachnida, we ought with its help to be able to answer some of the questions relating to the probable affinities of the Arachnida to the Insecta and to the Crustacea. A few words on this subject will still further emphasise the utility of the analytical method here advocated and adopted.

It is now almost universally admitted that all the different Arthropods are to be deduced from Chætopod Annelids. A question still to be decided, however, is, are they distinct and separate modifications, or have they branched off from one another, starting from some original Arthropod which linked them all with the Annelid? Many have been the proposed lines of descent of the Arthropods from some

common Annelidan ancestor. The chief use for these genealogical trees has been to emphasise and drive home the doctrine of descent; they have too often been nine-tenths guess work, the available facts being quite insufficient to warrant such elaborate conclusions. Now it seems to the present writer obvious that the only possible means of establishing without dispute the relationships of animals derived from a segmented ancestor is to analyse carefully the arrangements and distortions of the segments characteristic of each group, ascertaining, as far as possible, the physiological significance of these arrangements and distortions. As above stated, we must analyse each fusion qualitatively as well as quantitatively. It will only then be possible to see whether and how far modifications of segmentation can be deduced from one another or are distinct and separate. If they can in any way be deduced from one another, we should then have some solid foundation for a genealogical tree, if they are distinct and separate, then each group must have arisen separately and have no relationship to any other group besides that involved in common origin from Chætopod Annelids. Few more striking illustrations of the necessity of discovering and comparing what the present writer has termed the "essential morphology" of the Arthropod groups could possibly be given than the recent controversy as to whether the Arachnids are not related to the King-crab and its fossil allies. The anatomical and morphological resemblances on which this affinity was based were really remarkable, although it is true they were met by an almost equal number of dissimilarities. These latter, however, could not disprove the argument based upon the striking likenesses. The difficulty, however, vanishes if we set ourselves the task of ascertaining whether the essential morphology of the King-crab has any resemblance with the essential morphology of the Arachnida. No one, I think, will dispute the accuracy of this argument even if they are not satisfied with the present writer's published attempts to elucidate the essential morphologies in question. The results arrived at are the following: The Crustacea, among

which the King-crab finds its place, appear also to have originated by the adoption on the part of a Chætopod Annelid of a peculiar method of feeding. This consisted in bending round the mouth with its large prostomium or upper lip ventrally so that the limbs arranged along the body could rake the food into the ventral middle line and push it into the mouth. In process of time, various groups of those limbs which were nearest the mouth became specialised, some into jaws chewing the food within the mouth aperture, others into sensory feelers (antennæ).¹ There seems to me no possibility of connecting this method of modifying the anterior segments, this ventral bend of the first segment of the Crustacea with the initial specialisation of the ancestral Arachnid which as above sketched involved a tilting upwards and backwards of the first segment and the fusion of the upper and under lips to form a rigid sucking beak. The two must be regarded as separate and distinct modifications of their Annelidan ancestors. I repeat that, without such a qualitative analysis of the segmentation as is here suggested, I do not see how the question as to whether *Limulus* was an Arachnid or not, a question that for more than a decade has divided zoologists into two almost hostile camps, could ever have been finally settled, as I believe it now to be.

The insects are another group of Arthropods with which it has been thought the Arachnids might be associated. Some remarkable resemblances occur here again as in the cases of *Scorpio* and *Limulus*. The Insecta, like the Spiders, typically have waists and ten segments behind the waist. The number of segments in front of the waist does not correspond, but it was thought that, if a pair of small anterior antennæ had disappeared from the Arachnids, then the only difficulty would be removed. It is true that the Arachnids had typically no trace of a "head" marked off by a "neck," but some approach to a head region could, it was thought, be found in the helmet-like plate of *Galeodes*,

¹ The arguments on which this is based can be found in the author's book on the *Apodide*, *Nature Series*, 1892, and in two papers on the Trilobites in the *Q. Journ. Geol. Soc.*, vols. li., lii.

behind which came, as in the insects, a thoracic region with three pairs of limbs.

Here it will be seen that the whole stress is laid upon the quantitative differentiation of the segmentation; whereas as soon as the qualitative differentiation of the anterior segments of the two groups are compared it is seen at once that, in spite of all remarkable resemblances, the *Insecta* and the *Arachnida* have nothing in common except descent from a *Chætopod Annelid*.

The initial specialisation of the ancestral insect was undoubtedly also an adaptation to the method of feeding adopted. Unlike the *Arachnids*, the food was probably from the first supplied by the vegetable kingdom, and the limbs nearest to the mouth (except the first pair which became feelers) were specialised into biting jaws for tearing and crushing the edges of leaves or the surfaces of stalks. Highly developed locomotory powers were hardly needed for this method of feeding, so that an annelidan stage with only a head region showing the typical specialisation of the *Insecta* long persisted, and still persists, in the grub or caterpillar stages. We have no caterpillar or grub stage in the *Arachnids* because, being from the first carnivorous, the necessity of catching their prey required the development of highly specialised locomotory powers concurrently with the adoption and perfection of their method of feeding.

In this case again, then, the analytical method is emphatic against there having been any close affinity between the *Arachnida* and the *Insecta*. The three chief groups of the *Arthropoda*, the *Insecta*, the *Crustacea* and the *Arachnida* must be regarded as separate and distinct derivatives of the *Chætopod Annelids*.

I should like to add in conclusion that in thus insisting upon the necessity of solving the questions of affinity between the *Arthropods* by appeal to their "essential morphologies," by which I mean the peculiar structural modifications of their segments treated as physiological adaptations, I am aware that the method is not a new one; it lay in the direct path of morphological research. It needs emphasising, however, because the hopes which the study

of embryology held out to us of solving such questions by short cuts, hopes which have not been and, I fear, never will be realised, have drawn away attention too much from the analysis of adult forms. Every animal group contains in itself the record of its past, if we could decipher it. In some cases, such as those here dealt with, this is comparatively easy, but in others the record is so obscured that we may have to wait for fresh clues before we can unravel it.

In the meantime a more thorough comparative analysis of the forms of life at our disposal would not only bring us nearer to the solution of many an interesting problem, but would actually reveal to us clues which lie around us waiting to be recognised.

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H. M. BERNARD.

THE CELL-MEMBRANE.

I.

THE membrane by which the cells of vegetable tissues are bounded has generally been described by most authors as originating in a fairly uniform condition, and consisting at first at any rate of an almost or quite homogeneous sheet of cellulose. After its first formation it increases in surface and later in thickness, its composition remaining unchanged. Finally, in most cases it undergoes chemical transformations in its substance, becoming suberised, cutinised, lignified or mucilaginous. As generally described, therefore, cellulose alone must be regarded as the basis of the cell membrane and the modifications met with are due to changes in the cellulose, leading to the formation of other bodies, which are then found mixed with, and largely replacing, the latter.

The study of the cell-wall may thus be carried on under the two heads of the primitive membrane and such modifications of it as do not present the latter changes, and the modified membranes which are characteristic of woody, corky and mucilaginous cells.

In dealing with the former of these, what indeed may for purposes of discrimination be called "unchanged" cell-wall, it is well to recall the theories of its composition which have been advanced in recent years. Without entering into much detail we may mention the two hypotheses of Naegeli and Strasburger. According to the former the molecules of cellulose are aggregated together into quasi-crystalline groups, the micellæ, which are separated from each other by delicate films of water. According to Strasburger, the theory of the micellar aggregations is unnecessary and the structure is regarded as having a network arrangement, the meshes of the network containing water.

A later theory, advanced by Wiesner (1), has however much to recommend it, especially in the light of recent researches made upon the structure and chemical composition

of the wall. On this hypothesis the membrane is composed of a number of minute more or less rounded protoplasmic bodies, the dermatosomes, which so long as the cell-wall is immature and capable of growth are united together by delicate filaments, also composed of living matter. The cellulose is formed by these dermatosomes, which become embedded in it. New dermatosomes are continually constructed from the substance of the threads, so that the wall grows by a process of intercalation somewhat recalling Naegeli's intussusception. Successive layers of the membrane, however, may be formed so that the thickening of the adult wall may be due to apposition, while each layer is formed and increased by intercalation of dermatosomes.

The membrane which bounds two contiguous cells can more or less easily, as we shall see, be separated into two layers, often by merely mechanical methods, more frequently by chemical ones. Wiesner hence infers that the threads which connect the dermatosomes of two contiguous layers can be more easily ruptured than those which exist in the substance of the several layers of the wall.

The great value of this hypothesis will appear later. For the present we may note that according to it the whole substance of the membrane is in contact with protoplasm and not merely its internal surface. We have therefore the possibility of an active chemical change of the substance of the wall and not the probability of merely a decomposition of inert compounds, commonly described as a process of degradation.

The generally received idea of the cell-membrane is thus that of a homogeneous sheet of cellulose, formed in some way by a kind of secretion from the protoplasm, and only showing differentiation of its substance when it undergoes such a change as that of lignification or one of the others spoken of. In a tissue which has much-thickened walls, it is not difficult to recognise a middle layer lying between the cells in the substance of the wall, and to notice that the tissue can be disintegrated into its constituent cells by the process of solution of this layer. This *middle lamella*,

as it is usually called, is thus easily proved to be of different chemical composition from the remainder of the tissue.

Passing over for the present the question of the exact composition of this middle lamella in the much-modified cells of wood, sclerenchyma, etc., and turning to the young tissues, consisting of so-called unchanged cellulose and situated in the meristem of the apex of the axis, it is somewhat interesting to find that from their very commencement we can find evidence that the membrane is not homogeneous, but that whatever be its original substance something of the nature of a middle lamella can always be proved to exist. By appropriate solvents or treatment that will be described later, the thickness of the cell-membrane can be split into two and the young as well as the adult cells set free from each other, each retaining a complete cell-wall.

Besides this evidence of a material differing from cellulose forming part of the cell-wall from its early condition, we may note the presence in the intercellular spaces between the cells of parenchyma of a substance which Russow (2) and others described as "intercellular protoplasm," and which sometimes appears as a delicate lining to the space and sometimes takes the form of concretions of various shape and bulk, occasionally filling the intercellular passage. The true nature of this so-called intercellular protoplasm was by several botanists, notably Gardiner (3), determined to be much more allied to the substance of the cell-wall than to the protoplasm, though it does not give the micro-chemical reactions of cellulose.

The idea of the homogeneous nature of the cell-wall is thus seen to be at variance with the facts. It is strange that it should have been put forward so definitely up to quite recent years, as the study of the works of the botanists of forty to fifty years ago shows that there was then considerable discussion upon the subject.

As early as 1825, Braconnot (4) extracted from the roots of several plants, especially those of the turnip and carrot, from the bulbs of the onion, and from the stems and leaves of many herbaceous plants and trees, a certain feebly acid substance to which he gave the name of pectic acid. He

found it had a very wide distribution, not only in the vegetable kingdom, but in the substance of the individual plant. About the same time, or a little earlier, Payen (5) extracted from the root of *Ailanthus glandulosa* a peculiar vegetable jelly, which was closely related to, if not identical with, Braconnot's pectic acid.

These discoveries attracted the attention of various chemists and botanists to the subject, and during the next few years much was ascertained about pectic acid and its reactions. Vauquelin (6) in 1829 published an account of some methods of preparing it, and of a study of its properties.

During the next ten years, the work of Mulder (7) and Fremy (8) added to our information as to the chemical peculiarities of this body, and it soon appeared that it did not exist alone, but that at least one other body, *pectine*, was present also. Fremy later called attention to a third similar compound to which he did not at first give a name. He describes it as existing in fruits in the condition of a pulp, and being under the action of an acid rapidly converted into pectine. He distinguishes it carefully from cellulose, but says he is not able to separate the two, and hazards the opinion that it may be only pectine combined with a certain amount of lime. Later Fremy gave it the name of *pectose*.

The existence of bodies of this character in bulky tissues, and the possibility of their extraction by various solvents having been demonstrated, attention was directed to their whereabouts and their relationship to other elements of the tissues. They were soon associated with the cell-membranes, Mulder suggesting that though the form in which they exist in different parts of the plant is not known, it is probable that they are to be found in the thickening layers or depositions in the cell-wall. They can be extracted by alkalies from the cell-partitions.

Payen (9) in 1846 added another contribution to our knowledge by pointing out that in certain plants these pectic bodies exist in combination with the metals of the alkalies and alkaline earths, chiefly potassium and calcium. He located these compounds chiefly in the epidermal tissues,

the walls of the cells of which consist in large part of them. He held that the mineral salts were intercalated with other substances in the body of the cell-wall.

In a latter paper of Fremy's (10) written in 1848, he gives some account of his researches on the localisation of the bodies, which in his earlier work he had only indicated as existing in plant tissues. The hitherto unnamed substance he calls *pectose*, and declares it to be a constituent of the membrane so closely connected with the cellulose, and so easily changed by various reagents, that he had found it impossible to separate the two. Like cellulose it is insoluble in water. Fremy found it in the cell-walls of green fruits, such as the apple; in those of the roots of many plants especially such as are succulent, like the carrot and turnip; also in the fibres of the cortex of the axis. The pectine of other authors he considers to be a derivative of pectose.

Mulder extended the localisation of pectose to the collenchyma, and the thin-walled parenchyma of *Opuntia Brasiliensis*, and says that it occurs also in the external parts of the thickened walls of the laticiferous vessels or cells of *Euphorbia Caput-Medusæ*. Referring to Payen's researches he suggests that the pectic acid and calcic pectate of the latter are derivatives of pectose. Harting (11) suggests that the thickening matter of collenchyma, bast fibres and many other thickened parenchymatous cells, as well as the substance of most thin-walled cells consists of pectates or of pectose, which he supposes to be isomeric with pectic acid. Both these writers point out that while cellulose gives a blue colour in treatment with iodine and sulphuric acid pectose remains uncoloured under the same conditions.

These views, however, did not remain unchallenged. Other writers, among whom may be mentioned Poumarède and Figuier, denied the existence of pectic acid and considered that the wall is essentially homogeneous at first if not always, and that pectose and cellulose are essentially identical.

The substance forming the middle lamella being most easily recognisable and the latter layer being in so many

cases easily visible, the view arose that it consists of a sort of intercellular substance, or cement, joining contiguous cells together. This was advanced by von Mohl and supported by Mulder and Harting. These authors speak of its being very variable in composition and consisting very largely of pectose, filling the spaces between the cell-walls and penetrating into the inner layers. They also held that it forms the mass of the little projections or concretions which often extend into the intercellular passages. The layers internal to the middle lamella they regarded as chiefly cellulose.

Harting's conclusions on the formation and growth of the cell-wall are that the primary cell-wall forms the internal layer and that it becomes thickened by a process of intussusception from within outwards, the primary membrane being cellulose, while pectose is developed in the external region as the wall thickens. Von Mohl on the other hand holds that the intercellular substance as well as the pectose is not formed in the wall, but infiltrates into the cellulose, masking the reactions of the latter.

None of these writers agreed with Payen, that the so-called intercellular substance was composed of alkaline pectates. In a later paper, Payen (12) points out a difference that can be established in this substance in different places. He found he could disintegrate the tissues and separate the cells by treating pieces of the former by the successive action of dilute acids and alkalies. When so treated the lateral or radial walls could be easily dissolved, but not the tangential ones, so that the cells separated in radial chains. Hence he suggests that the lateral walls were separated by pectates and the others by laminæ of cellulose.

A method of distinguishing between cellulose and the various pectic bodies was pointed out by Fremy (13). This consisted in treating the tissue with ammonio-cupric sulphate (Schweizer's reagent). This reagent dissolves pure cellulose, while the group of pectic bodies remains apparently unaffected, though really much modified, insoluble cupric pectate being formed. Alkalies on the other hand do not affect cellulose, but dissolve the pectose by converting it into soluble pectates. He agrees with the other writers

that the pectose is situated under the internal layer of cellulose.

Kabsch (14) found that when a cell-membrane is swollen by the action of chlor-zinc-iod, the inner layers only take on the blue coloration of cellulose and that the middle lamella, or so-called intercellular substance, varies in different cases, sometimes remaining colourless, sometimes appearing yellow and occasionally taking a pale blue tinge. He consequently locates the pectic bodies in the middle layer and says that the inner layers consist only of cellulose. The middle lamella thickens as the cells grow older and the increase of the pectic material is due according to him to transformation of the substance of the primary membrane.

Vogl (15), who wrote at about the same time as Kabsch, takes the same view as to the origin of the pectic substances in the wall. His experiments were made chiefly on the roots of *Taraxacum officinale* and a species of *Podospermum*. He found that the innermost part or layer of the cell-membrane is composed of cellulose, next to which is found a layer of a mixture of cellulose and pectose, and concluded that the latter was derived from a process of transformation of the older part of the cell-wall. Most externally he identified the so-called intercellular substance, and he says he considers it due to a transformation of the cell-membrane proceeding from without inwards, the resulting material being pectose. Vogl accounts for the cell-fusions of the laticiferous vessels of those plants by a transformation of the original cellulose septa into a soluble pectose which becomes dissolved.

Wiesner (16) a year later, supporting the conclusions of Kabsch and Vogl, carries them further and applies them to the lignified and corky cells as well as the parenchyma. Working especially on the beet, he describes the fate of all the tissues, saying that all the cells alike begin by being the seat of pectic transformations from cellulose, and that while the cortical membranes remain in different stages of this metamorphosis this is in woody and suberised cells followed by further transformations, leading to the recognition of lignified and corky walls. There have thus been advanced

in the middle of the present century two opposite views of the composition of the wall or of the interpretation of the facts which have been observed.

A further controversy has been conducted with regard to the composition of the middle lamella or, as it was once called, the intercellular substance. The constant existence of this part of the membrane was first put forward by von Mohl (17) in 1835, and his views were much debated, Mayen opposing and Schleiden supporting them. Mulder and Harting, as mentioned above, distinguished pectose as forming at any rate part of this layer; Payen considered it formed of mineral pectates, principally those of calcium and potassium. Unger took up the position that its substance, differing from cellulose, was first formed in the tissue and that the cell-wall is a product of its transformation. Wigan (18) joins Mayen in denying its existence as a separate layer, and maintains that it is only a product of transformation due to chemical or physical modification of the oldest layers of the cell-membrane.

Schleiden on the other hand held it to be a true secretion of the cells which is caused to accumulate on the outside of the membrane. This, on the whole, is the view of Schacht, who says that like the cell-wall itself it is probably a product of the primordial utricle. Schacht writes very guardedly on the subject, suggesting that it is not certain that it increases in thickness as the cell-wall grows, but admitting that it seems thicker between adult cells than between young ones. Its reactions according to this author are that it is insoluble in concentrated sulphuric acid, soluble in alkalies, and destroyed by oxidising agents more rapidly than the cell-wall proper. Also, it is more capable than the latter of resisting putrefactive changes.

Unger's view of this substance being the antecedent of cellulose, is supported by Dippel in 1851 (19). This author describes it as consisting of a kind of jelly which persists as such for some time, cellulose being formed upon its surfaces. As development proceeds it becomes converted into cellulose, but even then it only turns brown and not blue on treatment with iodine and sulphuric acid, this difference of

behaviour being due to infiltrations of nitrogenous matters into it.

The intercellular substance was thus regarded by some of the older investigators as a primitive, jelly-like material, ultimately giving rise to cellulose, and by others as a product of secretion formed by the protoplasm and made to accumulate in the outer part of the membrane. By some its composition is not stated, especially by Schacht, which is rather surprising, as he carefully studied its reactions. As already mentioned, Mulder, Harting and Payen were agreed that pectic compounds entered into its structure. Dippel says it is not cellulose, but gives no opinion as to its nature.

In the writings of Naegeli, Sachs, and other later writers, the term "middle lamella" replaces "intercellular substance". It was proposed to call it the "primary membrane," but as this suggested a definite origin and was not exactly in line with the theory of growth by intussusception, which was then coming into favour, the term "middle lamella" came to be adopted. This certainly had in its favour the fact that it was essentially non-committal. The writers of this period leave its nature undetermined. Sanio (20) in 1873 speaks of it in *Pinus sylvestris* as "Zwischensubstanz" and describes it as a gelatinous material intercalated between the radial rows of the generating cells. Both Sanio and Dippel lean to the opinion that whatever its chemical nature it arises from decomposition of the original cell-wall, a view exactly opposite to that advanced by Unger some years previously.

When Wiesner put forward his hypothesis of the composition of the cell-wall he recognised the existence of this middle region and pointed out that very young cells could be separated easily by its severance; much more easily, indeed, than older ones, and concluded that the threads uniting the dermatosomes were much more easily ruptured in that region than in the other layers. The rupture could be caused in some cases by mere mechanical traction, in others by chemical reagents such as strong hydrochloric acid. Wiesner did not consider there was necessarily any chemical

difference, though he admitted it in certain cases, but even then he did not hold that it proceeded from any metamorphosis of the membrane which took place gradually at the periphery of the cell-walls.

The view that such chemical difference does exist and that the opinions of the earlier workers in this field are in the main accurate, receives some support from Van Tieghem's observations on the progress of putrefaction set up by bacteria. In his *Traité de Botanique* (21) he shows that *Bacillus Amylobacter* disintegrates vegetable tissues by dissolving the middle lamella. He says that the cellulose of the wall exists in two varieties, one of which is split up by the micro-organism into butyric acid, carbonic dioxide and hydrogen, while the other is unaffected. As Van Tieghem gives no reactions which are distinctive of these two varieties, it is clearly open to us to hold the view which accords with earlier investigations, namely, that the material dissolved by the bacterium is pectic in its nature and that pure cellulose is unaffected by it.

Besides the middle lamella, other modifications of the original wall need mention. Chief among these we have the so-called intercellular protoplasm of Russow (2). He described this substance as forming in certain cases a delicate membrane or lining-layer, coating the intercellular passages. This substance has been critically examined by Gardiner and by Schenck, both of whom deny its protoplasmic nature. Gardiner (3), relying on certain staining reagents, especially methylene blue, advanced the view that it is a product of cellulose decomposition, probably a kind of mucilage, and states that it varies very much in composition in different cases. Schenck held that it is of the same general nature as the middle lamella, but declined to give a more definite opinion as to its nature. Mangin considers it to be composed of a mixture of pectic bodies.

The rod-shaped filaments and concretions of various shapes which are found in the intercellular spaces of many of the Pteridophytes and in the integuments of the seeds of some of the Papilionaceæ have also been variously stated to be protoplasmic or to be formed of cutinised material.

There is great reason, however, to believe from Mangin's researches that these also are formed largely if not entirely of various pectic compounds.

The various investigations that have been summarised above, point unmistakably to the conclusion that the cell-wall is originally far from homogeneous, and that while cellulose enters very prominently into its composition there are present in it a number of other substances which have hitherto been somewhat loosely described under the names of pectose, pectine and compounds of pectic acid. The modifications of cell-wall which give rise to gums and mucilages, all of which are probably very complex, may well be derived from these and not from the cellulose constituent at all. At the same time it must not be overlooked that several modifications of so-called cellulose exist, differing from each other possibly in the degree of their hydration.

In considering the composition of cell-wall, as far as it has been determined at present, the researches of Mangin (22) on the subject are most complete and of the first importance. Till his memoir appeared the whole group of pectic compounds was ill-defined, and nothing very definite was known as to the distribution in plant cell-walls of most of them.

These compounds can now be arranged in two series, one of the latter comprising bodies of a neutral reaction, while those of the other are feeble acids. In each there are probably several members, which show among them every stage of physical condition between absolute insolubility and complete solubility in water, the intermediate bodies exhibiting gelatinous stages, characterised by the power of absorbing water in a greater or less degree.

Of the neutral series the two extremes are presented by *Pectose* and *Pectine*. The former is insoluble in water and closely associated with cellulose in the substance of the membranes; the latter is soluble in water and forms a jelly with more or less facility.

In the other series the two most noteworthy members are Pectic and Metapectic Acids. The former generally exists in the membranes in combination with the metals of

the alkaline earths, especially calcium; when in the free state it is insoluble in water. Metapectic acid is soluble in water without forming a jelly. The two series are closely related to each other, for by the action of heat, acids and alkalies the various members of both can be prepared from pectose. The final product of the action of the reagents is the freely soluble metapectic acid.

Mangin gives their distinctive reactions as under:—

Pectose.—The actual properties of this substance are not at all easy to ascertain, nor can they be said to be well known. The material is so closely associated with cellulose that it cannot be prepared pure at present. The reagents that separate it from cellulose convert it either into pectine or into pectic acid, the former being soluble in water, the latter in alkalies. The membrane can be shown to contain the two constituents by the action of Schweizer's reagent, which when used with the proper precautions dissolves out the cellulose and leaves the framework of the cell apparently unaltered; it then consists, however, not of pure pectose, but of a compound of pectic acid with the copper of the reagent.

Pectine.—This body swells up and dissolves in water, giving a viscid liquid which is very difficult to filter and which soon forms a jelly. This is the body which Fremy found in ripe fruits, and it exists in many mucilages. It gives no precipitate with neutral acetate of lead, but is thrown down by the basic acetate in the form of white flocks. If boiled for several hours in water it is converted into an isomer, *parapectine*, which is precipitated by the neutral acetate. Further boiling with dilute acids converts it into *metapectine* which is precipitated by barium chloride.

Pectic acid.—This body is insoluble in water, alcohol and acids; it forms soluble pectates with alkalies and insoluble ones with the metals of the alkaline earths, of which calcic pectate is most widely distributed. It dissolves in solutions of alkaline salts, such as the carbonates of sodium and potassium, stannates, alkaline phosphates, and most organic ammoniacal salts, forming with them double salts which gelatinise more or less freely with water. Its solutions in

alkaline carbonates are mucilaginous and difficult to filter, while when oxalate of ammonia is the solvent it is perfectly fluid and filters readily.

Metapectic acid.—This is a body with an acid reaction, freely soluble in water, and forming soluble salts with all bases, especially calcium and barium, which precipitate pectic acid. Metapectates warmed with an excess of alkali take a yellow colour. This body and its compounds approach the gums in their composition.

Metapectic acid can be prepared from either pectine or pectic acid by boiling with excess of alkali. Acted upon by sulphuric acid it splits up into a dextrorotatory crystallisable sugar, apparently identical with arabinose, and into a little-known organic acid, indicating by this behaviour some relationship to the group of the glucosides.

The reactions just given clearly show that these pectic bodies form a group quite distinct from the celluloses which are known. The ease with which they are altered by the reagents used for their extraction readily marks them off from the latter, as do the products of their oxidation. If warmed with nitric acid, instead of being oxidised to oxalic acid like the carbohydrates, they give rise to mucic acid. They are further all insoluble in Schweizer's reagent and they give no blue coloration with iodine in any combination.

In endeavouring to ascertain the various ways in which these bodies are associated with cellulose in the cell-membrane, Mangin relied partly upon staining reagents and partly upon the action of various solutions in which one or other of the constituents of the wall are soluble. His investigations do not take into account the modifications which lignified, suberised or mucilaginous walls present, but only those in which the membrane has been considered to consist of unchanged cellulose.

A marked difference between cellulose and pectic bodies soon comes out in studying the action of stains upon them. Cellulose acts as a feeble base and takes up, therefore, acid stains, particularly those containing nitrogen. Pectic compounds, on the other hand, act as acids and require basic stains.

Hæmatoxylin, methylene blue, vesuvian brown and quinolin blue stain the pectic constituents of the wall and not the cellulose as has hitherto been supposed. The composition of the wall in any case can be better ascertained, however, by the action of solvents. If sections be placed in freshly prepared Schweizer's solution and left for several days, the fluid being renewed daily, the cellulose becomes gradually dissolved, complete removal of it being effected in the soft tissues in about three to four days. The sections must then be washed several times with water and later with a solution of acetic acid, containing from three to five per cent. of the latter, till all trace of the copper has disappeared. The shapes of the cells can then be seen to be unaltered, although naturally the sections have become very fragile. That the cellulose has been completely extracted is shown by treating the tissue with iodine and phosphoric acid, when the walls become pale yellow instead of blue. If the sections have been rather thick the cellulose will have disappeared from the membrane, but as the solution of this substance in Schweizer's reagent is slightly viscid, it will not all have been removed from the sections by the washing with water, and the subsequent treatment with the dilute acetic acid will have precipitated it in little clots in the intercellular spaces or sometimes in the interior of the cells. These little masses will, after the treatment with the iodine and phosphoric acid, stand out as blue patches among the yellow membranes. If now the stains for which the pectic bodies have an affinity be applied to the sections, the membranes all take them up freely.

The pectic compound thus remaining after removal of the cellulose is not unchanged pectose, but has been converted in great part into pectic acid; for if the section be irrigated with ammoniacal oxalate, in which this acid is soluble, all the membranes rapidly disappear. If instead of the oxalate the walls be dissolved in ammonia and then the latter be neutralised by dilute acetic acid, a gelatinous precipitate falls, which can be stained with a basic stain such as methylene blue.

Another method of demonstrating the mixed nature of

the wall consists in dissolving away the pectose and leaving the cellulose. Sections of the tissue may be boiled for half an hour with two per cent. solution of hydrochloric acid. After repeated washings in water, they should be again boiled for some time in two per cent. solution of the hydrate of potassium or sodium and again washed thoroughly. The tissue will then stain a deep blue with iodine and phosphoric acid, but not with basic stains.

There is only one substance which behaves like the pectic compounds with basic stains—the *gelose* of the Algæ. This can be distinguished from the former bodies by being soluble in hydrochloric acid diluted with an equal volume of water, but being insoluble in alkalies.

By means of these methods of procedure, Mangin has ascertained that in Phanerogams, Pteridophytes and Muscineæ hardly any soft tissue is devoid of pectic bodies in its cell-walls. These are found conspicuously present in parenchyma, collenchyma, bast and meristem tissues, pectic acid and pectose being the compounds generally occurring. Pectic acid, as Payen pointed out, usually exists in the tissues in combination with calcium as calcic pectate. Mangin demonstrated this fact by steeping the tissue, cut into small pieces, in dilute hydrochlorate acid, or preferably in a mixture of one part hydrochloric acid and three parts of alcohol. The pectate was decomposed, the calcium being converted into calcium chloride and the pectic acid liberated. This being insoluble was washed with water till all the hydrochloric acid was removed. It was then dissolved in a weak solution of potassic hydrate or carbonate and the solution filtered. On neutralising with a dilute acid the pectic acid was thrown down in gelatinous flocks. Mangin found, as Payen had done before, that the middle lamella, von Mohl's "intercellular substance," consists almost or quite entirely of calcic pectate, which serves as a kind of cementing medium, joining contiguous cells together. When by any reagent it is dissolved, the cells separate from each other.

The dissociation of the tissues by the process of dissolving the calcic pectate can be effected more gradually

by a prolonged soaking in cold alkaline solutions, or in Schweizer's reagent; by this treatment double pectates which are soluble and gelatinisable are formed.

The pectic body which exists in the thickness of the wall survives this dissociating treatment and is probably the pectose of Fremy. What are the relationships between it and the cellulose have not yet been determined, but there is a very intimate association between the two, and this probably a mechanical one, as they can be separated, but only by methods which materially alter if they do not destroy one or both. Mangin's mode of preparation of it has been already described.

The pectose and calcic pectate are thus found to be both present in soft delicate tissues, but in different proportions. In the young cells of meristems there is but little calcic pectate, while pectose is in larger proportion. It is not certain that in these cells it is mechanically combined with or embedded in a cellulose matrix; it may be united more closely with it, forming a compound comparable to a glucoside which splits up under the action of an acid, yielding cellulose and pectic acid.

In older cells, among which intercellular spaces or passages have appeared, the proportion of calcic pectate is more prominent, though even in the younger ones the limiting layer is composed of this substance. This outermost layer is quite free from cellulose. The calcic pectate often collects over the surfaces of the intercellular spaces, being, in fact, a continuation of the middle lamella of the wall which has split in the formation of the passage. It is easy to see also how the small plugs or concretions which are often found in such spaces may be formed of the same material.

Though these two bodies are the forms of pectic compounds which are most widespread, many intermediate modifications are met with which present their own peculiarities with respect to solubility, affinity for bases, etc. Thus the pectates which form the middle lamella are sometimes gelatinisable, swelling up in water. Such a variety is found between the cells of the lacunar parenchyma of *Calla*

athiopica, in the peduncle of *Narcissus pseudo-Narcissus*, etc. In *Narcissus* it occurs in the intercellular spaces.

As the wall of the young cell increases in thickness the secondary laminae show a certain difference in composition, pectoses being most abundant in the layers nearest to the middle lamella and cellulose most prominent in the newest layers nearest to the protoplasm of the cell.

The dissociation of the young tissues shows the interesting peculiarity indicated by Payen, the substance joining the cells not being the same throughout. If transverse sections be taken, the dissociation easily takes place in the radial direction but not so readily in the tangential one, so that radial rows of cells are separated from each other. If a longitudinal section of the growing apex of a stem or root be examined the lines of easiest cleavage can be seen to converge towards the initial cells of the apex, each group being wrapped round by a thin membrane.

We may now turn to the question of the composition of the primitive cell-wall. Is this originally homogeneous? If so, it may be regarded as being from the first formed of an intimate mixture of cellulose and pectose, forming a kind of *cellulose* approaching a glucoside in nature. On this hypothesis it becomes thickened with layers of the same nature, and the middle lamella is not at first present as a differentiated region. Soon by a kind of intussusception a deposit of calcic pectate is produced in the middle of the wall; or such a deposit may arise from a decomposition of the pectose under the influence of the acid sap and the infiltration of soluble calcic salts.

On the other hand the primitive wall may be from the first heterogeneous the first lamina being formed of calcic pectate, which becomes very speedily covered on its two faces by layers of the mixture of cellulose and pectose. On this hypothesis the middle lamella is universally present, and in fact constitutes the "primary membrane" of the writers immediately preceding Naegeli.

Whichever hypothesis may be adopted there is no doubt that in soft tissues at the moment when cell division ceases the wall can be shown to consist of a middle lamella of

insoluble pectates, containing no cellulose, and lined on each side by mixed layers of cellulose and pectose. From that point onwards it undergoes throughout its substance continuous transformations which modify the disposition of its constituent substances, the middle lamella becoming conspicuously increased in amount.

In this connection it is well to remember Wiesner's hypothesis of the dermatosomes in the wall, as it is evident that such transformations of material may well be brought about under the influence of such protoplasmic bodies in the interior of the membrane.

The mode of deposit of the projections or concretions of calcic pectate may perhaps aid us in forming a true conception of what takes place. These pectates gradually tend towards the outside of the membrane, passing possibly as soluble pectic acid in its substance, and being combined with the metallic base at the external surface or in the intercellular space. In the young growing cell, just behind the zone of cell division at the growing point there is the maximum of turgidity or osmotic pressure. It is quite conceivable that in a free cell this is sufficient to cause a stream of soluble bodies to pass across the substance of the cell membrane from within outwards. This indeed would lead to the extrusion of such soluble pectates, or pectic acid, which may be well formed from the pectose in the membrane by the action of the dilute acid of the cell-sap, into the space around the cell, or in a tissue, into any intercellular passage. But in the case where the cells are not free, but have their neighbours pressing upon them, as they have in the young part of the growing zone, any membrane will be subject to a pressure from each side, owing to the turgidity of the contiguous cells. In this case the stream of pectates would not pass out of the cell, but would tend to accumulate in the middle line between the two pressures, in the region that is where the middle lamella speedily becomes recognisable.

In connection with the formation of the calcic salt from the acid body, we may recall Fremy's observations on the ferment which he discovered in the root of the carrot.

This has the property of causing the soluble pectic bodies to gelatinise. Recently Bertrand and Mallevre (23) have again investigated the action of this ferment *pectase*, and have discovered that its action is not to cause the formation of pectic acid as Fremy supposed, but a pectate of calcium. By careful experiments they have shown that if Fremy's mode of preparation of pectine be followed, and then the pectine be carefully washed with a mixture of alcohol and hydrochloric acid till all traces of calcium are removed, a solution of such pectine will not clot on the addition of pectase which is also free from lime salts. If a small quantity of calcic chloride be now added, clotting takes place gradually, the length of time required being proportional to the quantity of the calcium salt used. The formation of calcic pectate which can thus be induced outside the plant by ordinary laboratory methods may well represent what goes on in the plant itself. It is well known that in the case of many of the unorganised ferments the enzyme carries out a process which can quite easily be effected by the protoplasm alone. If we have as Wiesner suggests a kind of framework of protoplasm throughout the whole of the unaltered cell-membrane, and we have slowly passing into or through the wall, under the influence of the internal osmotic pressure, a stream containing soluble pectates, and the usual mineral bodies of the cell sap, in which calcium salts must always be included, there seems no difficulty in explaining the deposition of calcic pectate in the form of a definite lamina where the pressures from two contiguous cells oppose each other.

Mangin in his paper rather holds to the other view, judging from experiments in rupturing the young cell-membranes, that there is first formed a layer of pectates, that indeed the first microsomata that are accumulated across the cell spindle have this composition.

The formation of intercellular spaces probably depends upon the behaviour of the calcic pectate. During the period of cell division the cells contain only protoplasm with a little water and there is little internal pressure. The cells are in close contact with each other and polyhedral or

cubical in shape. As the cells are left behind, and from the growing rather than the dividing zone, they become vacuolated and osmotic pressure gradually becomes considerable. When the growth of the cells in turn has ceased, the osmotic pressure causes the membrane to be in a state of tension, so that the limit of its extensibility is reached and its elasticity is equal to the stretching force inside. At this time the calcic pectate at the angles of the polyhedral cells becomes gelatinous and under the strain it gives way at the points where the gelatinisation is complete. The middle lamella in fact ruptures at the angles, while the other layers remain intact.

This mode of regarding the formation of intercellular passages enables us easily to understand how some of them become coated with a thin layer of pectates. Into some of them at the angles the gelatinised middle lamella can be seen to extrude, forming little plugs or projections. There may further be a continuation of the passage across the membrane of the soluble pectates, which, not now being balanced by a similar stream from an opposing cell, make their way to the exterior of the membrane and appear as a thin coating over the surface of the passage. Hence may also be formed the curious projections of pectates which have been found as already mentioned in the parenchyma of many *Pteridophytes* and other plants.

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J. REYNOLDS GREEN.

THE COAGULATION OF THE BLOOD.

THIRD PAPER.

HAMMARSTEN'S theory of the cause of blood-clotting was formulated over twenty years ago, and it has stood the severe test of time, before which so many physiological theories fall to the ground. It still continues to be the best working theory we have on the subject. Put briefly it runs as follows :—

In the living blood, a proteid of the globulin class called fibrinogen exists in solution. When the blood is shed, the fibrinogen molecule is split into two parts; one part is a globulin which remains in solution, the other and more important part is the insoluble proteid called fibrin, which entangles the corpuscles and produces the clot. This decomposition of fibrinogen is accomplished by the fibrin-ferment which is one of the products of the disintegration of white corpuscles, blood-tablets and other protoplasmic structures that occurs when the blood leaves the vessels or comes into contact with foreign matter.

This theory replaced the older one of Alex. Schmidt who taught that fibrinogen and paraglobulin were both necessary for the formation of fibrin.

Since Hammarsten's theory was formulated investigators have not been idle, and in two papers published in this Journal,¹ I have given an account of the principal work that has been done in relation to the question. This work includes that of Wooldridge who introduced the important method of studying coagulation in the blood-vessels themselves, and in not being content with mere experiments *in vitro*. He showed that the "tissue-fibrinogens," substances obtainable from most of the cellular organs of the body, will, when injected into the circulation of a living animal, produce intravascular coagulation. These tissue-fibrinogens are nucleo-proteids, and fibrin-ferment belongs

¹ Vol. ii., p. 369; vol. iii., p. 127.

to the same class of substances.¹ The other principal new fact that has been discovered is the great importance of calcium salts in the process, though as to the exact way in which these salts exercise their influence there is considerable diversity of opinion.

My reason for once more returning to this subject is that within the last few months Hammarsten has broken the silence of twenty years, and once more attacked the problem. In the paper² he has published, one notes again the hand of the master; there is the same thoroughness and lucidity which were so evident in his older work, though it is interesting to note that experiments *in vitro* are still exclusively relied on to support his conclusions. The special subject with which he deals is the rôle played by calcium salts in the production of fibrin from fibrinogen, and his endeavour to settle the differences between rival theories is attended with considerable success. I propose to devote the remainder of this paper to a brief consideration of his experiments and their results.

Though Hammarsten himself, Green, Ringer and Sainsbury, Freund and others had noticed the accelerating action of salts of lime in promoting coagulation, it was not until Arthus discovered that coagulation can be prevented by decalcifying the blood by the addition of an alkaline oxalate, and Pekelharing had followed up this work with new experiments, that the calcium salts were recognised universally as a *sine quâ non* in the process of blood-clotting.

There are two possible stages in the process where the favouring action of calcium salts might come in; one of these is in the genesis of the fibrin-ferment, and the other is in the action of the fibrin-ferment in converting fibrinogen into fibrin. Arthus believes that there is a very close resemblance between the clotting of milk by rennet, and that of blood by fibrin-ferment. In the curdling of milk by rennet, the first action is the action of the ferment itself producing a

¹For the identification of fibrin-ferment as a nucleo-proteid see Pekelharing *Centralb. f. Physiol.*, vol. ix., p. 102, 1895; Halliburton, *Journal of Physiol.*, vol. xviii., p. 314, 1895.

²*Zeitsch. f. Physiol. Chem.*, vol. xxii., p. 333, 1896.

change in the proteid called caseinogen ; the second stage is due to calcium salts, which precipitate the changed caseinogen, as the curd of casein. Fibrin is similarly believed to be a calcium compound of fibrinogen. On the other hand, Pekelharing showed that calcium salts have the additional action of assisting the formation of fibrin-ferment from its precursor or zymogen. The main outcome of Hammarsten's work is to show that this is the only part that the soluble calcium salts of the plasma play. They are undoubtedly essential for coagulation, but after fibrin-ferment has once been formed their presence is no longer necessary. Or to put it another way, and adopt a new nomenclature : in the living blood no *thrombin* or fibrin-ferment is present ; that substance exists in the form of a zymogen, which may be termed *pro-thrombin* ; calcium salts act by converting prothrombin into thrombin.

Any one who has ever tried to prevent coagulation in blood by adding a soluble oxalate to it immediately it is shed will know that they will often fail. This is because they are not quick enough. If the oxalate is mixed with the blood sufficiently rapidly, it will prevent the formation of thrombin ; but if there is the least delay, prothrombin will pass into the condition of thrombin, and no amount of oxalate subsequently added will prevent the thrombin or fibrin-ferment from converting fibrinogen into fibrin.

In the present research, Hammarsten prepared specimens of oxalated plasma, specimens of oxalated solution of fibrinogen, specimens of oxalated solution of fibrin-ferment, and specimens of oxalated serum, which is practically a solution of fibrin-ferment with numerous other things as well. On mixing together such solutions of fibrinogen with such solutions of fibrin-ferment he always obtained, and frequently rapidly obtained, a typical and abundant formation of fibrin.

In this connection it is important to notice that oxalated preparations of this kind are not in the strictest sense of the word, decalcified. They are only decalcified in what Hammarsten calls Arthus' sense of the word. That is, the oxalate added is unable to combine with and displace the calcium which is directly in union with proteid matter.

This was previously pointed out by Schäfer¹ in connection with this same question, and by Ringer² in connection with the contractility of the cardiac muscle. No reference is made by Hammarsten to these researches.

Other investigators who have tackled the question of calcium salts in their relationship to blood coagulation are Alex. Schmidt and Lilienfeld, and the points of difference between these workers and those previously mentioned are cleared up by Hammarsten in the following way:—

The view of Alex. Schmidt, that lime salts act qualitatively like other neutral salts such as sodium chloride in promoting coagulation, though in the quantitative sense they are admittedly more powerful, is incorrect. Arthus is unquestionably right when he ascribes to calcium salts a definite and specific action. The action of soluble oxalates is also definite and specific, for by precipitating the calcium salts it neutralises this specific action, and thus inhibits the coagulation of the blood. Here again Arthus is right, and Schmidt who supposes that alkaline oxalates act in the same manner as excess of other salts of the alkalis in preventing coagulation, is wrong. Arthus, however, goes wrong in the specific action he attributes to the calcium salts. They are not necessary for the change of fibrinogen into fibrin. If a sufficient quantity of fibrin-ferment is present, fibrin-forming goes on as typically and abundantly in solutions which do not contain soluble lime salts (these having been removed by oxalating), as in those which do contain such salts. In this way the analogy drawn by Arthus between fibrinogen and fibrin on the one hand, and caseinogen and casein on the other breaks down. The specific and only action of the lime salts is that discovered by Pekelharing, in producing the genesis of thrombin or fibrin-ferment, from its precursor, prothrombin. Pekelharing's experiment that the blood-plasma contains a material

¹ In a preliminary note to the Physiological Society ("Proc. Physiol. Soc.," p. 18, 1895, in *Journal of Physiology*, vol. xvii.) Schäfer arrived at much the same conclusions regarding this point, and regarding Lilienfeld's thrombosin to be immediately alluded to, that Hammarsten presents more elaborately in his present contribution to the subject.

² *Practitioner*, vol. xxiv., p. 81.

(nucleo-proteid in nature, prothrombin by name) which is not fibrin-ferment, but which by the action of soluble lime salts becomes converted into another substance (also essentially nucleo-proteid in nature, but thrombin by name) is easily confirmed. This second substance is a powerful accelerator of the coagulation process, and is in fact fibrin-ferment.

Lilienfeld's facts and theories are wrong throughout. This worker stated that if he took a solution of fibrinogen, and added to it some acetic acid, he obtained a precipitate of a new material which he called thrombosin; if he then added calcium salts to a solution of thrombosin he obtained a formation of fibrin. Thrombosin may also be precipitated from a fibrinogen solution by nucleic acid, and this is what he considered to occur in actual coagulation; the nucleic acid of the nucleo-proteid in the blood first separates thrombosin from fibrinogen, and then the thrombosin is precipitated as fibrin by calcium.

It has already been stated that Schäfer could not confirm this, and no more can Hammarsten. The so-called thrombosin is no new substance, it is simply fibrinogen which is partially precipitable by the acids just mentioned. When it is dissolved in saline solution and a soluble calcium salt added there is neither coagulation nor precipitation if fibrin-ferment is absent, though if fibrin-ferment is present, even though soluble lime salts are absent, fibrin is formed in the usual way.

It may be added that Lilienfeld is equally wrong when he distinguishes between nucleo-proteid and fibrin-ferment. Fibrin-ferment is not a globulin; it is a nucleo-proteid. It is not the result of fibrin formation as Lilienfeld states, but all the facts at present at our disposal point to it as the main cause of the transformation of fibrinogen into fibrin.

Underlying the theories of Arthus, Pekelharing and Lilienfeld there is one fallacy common to all. All look upon fibrin as a calcium compound of fibrinogen or of some derivative of fibrinogen. Hammarsten states this is not the case. Both fibrin and fibrinogen contain calcium, but there is the same amount of that element in each.

W. D. HALLIBURTON.

ON THE RELATION BETWEEN THE FORM AND THE METABOLISM OF THE CELL.

THE problem to which I wish to draw the attention of biologists in the following paper is one which, no doubt, has already excited a certain amount of interest, but which has not yet, as far as I know, been made the subject of special research. I allude to the question as to the relationship which may exist between the form and the metabolism of the cell. This subject is of peculiar importance at the present time, when morphologists are busy discussing the special mechanical factors of organic formation; its consideration is therefore likely to lead to wider views on the whole subject of development or rather of form-evolution than are usually entertained.

The problem of the organic formation of the body is not purely morphological; it has also a physiological aspect, inasmuch as the full play of the vital processes of an organism is the one necessary condition of its proper and complete development. The ontogenetic evolution of the body and its vital processes are thus inseparably connected, and it is impossible to understand its mechanical structure unless its physiology be also taken into account. I am inclined to emphasise this point, as it seems to me that too great prominence is now often given to the morphological aspect of the question, whereas metabolism, the fundamental process on which all vital phenomena are based, is almost overlooked as a factor in the problem.

Now it has long been recognised as a physiological fact that all the vital phenomena of an organism are only different expressions of its metabolism; consequently all the form-changes of an organism, being among its vital processes, must, in the long run, be the outcome of its own characteristic metabolism.

The remarkable fact that this evident truth has been so little taken into consideration can only be accounted for by the difficulty of combining the two groups of pheno-

mena—metabolism and organic formation. For example, metabolism is practically inconceivable without a fluid condition of the substance undergoing change, while, on the other hand, the idea of a definite form involuntarily suggests a fixed position of the particles of matter of which the organism is composed. This difficulty, however, is merely superficial, and vanishes as soon as we examine the two seemingly irreconcilable facts. A fluid stratum is certainly a requisite of metabolism. In the words of the ancient alchemists, *corpora non agunt nisi humida*. Only gases or dissolved matter can enter into the chemical relations required in the metabolism of an organism.

This truth ought not to be ignored, as it has been by those who have maintained that the cell substance is more or less compact and solid. Many have regarded the protoplasm of a cell, including its nucleus, as a sponge-like network, others, merely recently, as a thread-like structure, composed of numberless fibres. To Berthold and Bütschli, however, belongs the credit of strongly insisting upon the fluid nature of protoplasm. Those who hold the opposite view base it solely on the examination of dead and preserved objects; it is difficult to imagine how any one can maintain it who has studied the life processes in living cells, *e.g.*, the protoplasmic movement in a creeping Amoeba, the many-branched system of currents in a Myxomycete plasmodium, or the rotation of the protoplasm in a plant cell. On the other hand, there can be no doubt that protoplasm, although essentially a fluid, does contain some more solid and firm elements, *i.e.*, it is a compound of substances of various consistencies.

When we find ourselves face to face with the question, "What are we to consider as actually living in living matter?" we have but one criterion to assist us to a decision, and that is metabolism. Only where there is metabolism is there life. This is the A B C of physiology. Hence, we can only call those particles alive which are undergoing chemical changes. We must consider as not alive, in the most restricted sense of the word, all matter which is not at the moment chemically active, even though,

like reserve material, it may be drawn, when required, into the metabolism. For instance the starch granule in the plant cell, the glycogen particle in the animal cell, so long as they remain without chemical change, as reserve material in the protoplasm, are not living. They only become living substances when, decomposed and dissolved, they take part in metabolism. The inner and outer skeletal portions of the cell, and also certain solid intercellular substances such as bone and cartilage cannot be considered as living, in the real sense of the word.

There can, however, be little doubt that, in many cells, certain parts are in a state of active metabolism in spite of possessing a form so unvarying that it gives the characteristic stamp to the whole cell. Striped and smooth muscle fibre, the ciliated epithelial cell, and the infusorian cell are well-known examples of this. The question then arises: "How is it possible that a fluid mass such as, for instance, a ciliated cell, can have an unvarying and complicated form?" The more or less rigid connection of the particles which we necessarily associate with solidity cannot be admitted since that would make metabolism impossible. In attempting to solve this question, some have assumed that, in cells which possess an unvarying form, the protoplasm is of a medium consistence, half fluid, half solid, and there is little to be said against this suggestion. The degree of fluidity, *i.e.*, of mobility of the particles, varies greatly in different fluids, and it is therefore possible that, in some cases, living matter has the characteristics of a very thick fluid. On the other hand, a high degree of mobility of the particles is a *sine qua non* for active metabolism, which not only extends over the surface but penetrates the cell in its entirety. The presence of metabolism in such comparatively rigid forms as a muscle fibril or a ciliated cell implies great activity of the particles, and thus the assumption just mentioned, *viz.*, that of a semi-solid, semi-fluid consistency on the part of the protoplasm is of no real assistance in an attempt to reconcile the apparently contradictory facts of the active movement of the component particles and unvarying form.

In this case as well as in that of many other physio-

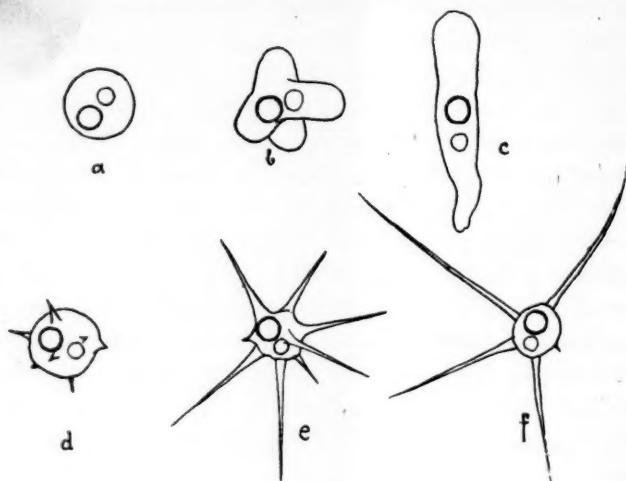
logical problems it is advisable first of all to study the primitive conditions exhibited by the lower cells, such, for instance, as are revealed to us by masses of naked protoplasm, *e.g.*, by the Amoeba. Such cells, in spite of, or rather just because of, their varying form appear to me to be capable of explaining not a few of the elementary problems of the organic formation of the body.

The organic form of the Amoeba is controlled by two principal factors, one physical and the other chemical. Physically, the Amoeba cell possesses the qualities of a fluid. This drop of fluid, however, is constantly exchanging its matter with the surrounding medium. As a fluid, the body of the Amoeba is subject to the physical laws which govern fluids and, if considered as existing solely under the influence of these laws, could well be supposed to assume a definite fixed form, let us say that of a sphere. This form the body of the Amoeba would permanently retain if the conditions remained unaltered. Change, however, will take place as soon as it enters into chemical relations with the surrounding medium. In these chemical relations, in other words in metabolism, then, we have the cause of the movement, of the flowing onwards and of the changes of shape of the Amoeba.

It is worth while to look a little more closely into the relations between the metabolism of the Amoeba and its change of shape. Let us take first, by way of example, the relation between respiration and the change of form. In connection with a previous observation by Kühne, I have elsewhere shown that a constant connection exists between the extension of the pseudopodia of the Amoeba and the amount of oxygen in the medium. With the withdrawal of oxygen the formation of pseudopodia and consequently the change of shape ceases; on the return of oxygen it recommences. This fact appeared to me to be of such fundamental importance that I repeated Kühne's experiments on large Rhizopods from the Red Sea, these being in many respects specially suited for the purpose. My results agreed entirely with those obtained by Kühne. The expansion of the long, straight, thread-like pseudopodia, such as the long rays which stream outwards from the cell of the Orbitolites,

ceased with the withdrawal of oxygen. The protoplasmic movements were arrested and the Rhizopod remained motionless until a fresh supply of oxygen caused the pseudopodia once more to expand. The formation of pseudopodia, and consequently the change of shape of the body, is thus evidently in the highest degree dependent on the supply of oxygen. On the other hand, total retraction of the pseudopodia can be caused by the introduction of certain acids, alkalies, or salts, into the medium surrounding the body. Sulphuric acid, potassium hydrate, or potassium sulphate, of a certain degree of concentration, added to the water containing an Amoeba at once cause retraction of the pseudopodia.

The dependence of the form of the organism upon its chemical relations with the surrounding medium is also clearly shown by the following facts, which a series of experiments have recently enabled me to demonstrate. Amoebæ, as is well known, are usually divided into different species



DIFFERENT FORMS OF THE SAME SPECIES OF AMOEBA.

- a.—Spherical, during strong excitation.
- b.—Beginning to move in the form of *Amoeba proteus*.
- c.—Usual form of *Amoeba limax*.
- d.—Beginning to assume the form of *Amoeba radiosa* after addition to the water of Potassium hydrate.
- e, f.—Form of *Amoeba radiosa* under the influence of potassium hydrate.

according to the form of their pseudopodia. The *Amoeba proteus* is distinguished by broad finger-shaped pseudo-

podia; the *Amoeba radiosa* resembles a ball with numbers of thorn-shaped pseudopodia; the *Amoeba limax* consists, as it were, of one long club-shaped pseudopod which flows almost entirely in the direction of its longitudinal axis. It is an interesting fact that one and the same Amoeba may for a certain period be an *Amoeba limax*, then for another period an *Amoeba radiosa*, *i.e.*, it may assume two entirely different outward forms according to the condition of the surrounding medium.

A large number of small and very active Amoeba of the *limax* species (*c.*) were placed in a culture glass in neutral water. When, by a small addition of potassium hydrate, I rendered the water slightly alkaline, all the Amoeba, after the lapse of a quarter of an hour, assumed the typical form of the *A. radiosa* (*e, f.*) and retained this shape without showing the least interruption of their vitality.

Again, an *Amoeba proteus* having finger-shaped pseudopodia spreading in all directions, may be made to assume the form of an *A. limax*. If a chemical which causes the expansion of the pseudopodia be added so as to act only on one side, or if it be attracted by oxygen or food in one definite direction, the shape of the animal changes, *i.e.*, it assumes the form of one large pseudopodium extended towards the point from which the new influence emanates. The whole mass of the organism flows along this one pseudopodium, creeping towards the oxygen or food in the shape of a thick club, this shape being retained as long as its metabolism is influenced from the side. In spite of this rigidity of the form the whole substance of the body is in active movement; a current flows, as in a fountain, forwards in the longitudinal axis and backwards at the circumference.

These observations show plainly that, in a protoplasmic body which varies in shape, the form is determined by the different conditions and changes of the metabolism, and that every modification in the latter is associated with some definite shape. If a certain condition of the metabolism continues for a length of time, the form of body appertaining to it will also continue, even though, as in the case of

the Amoeba just described, the substance of the body may be in constant movement.

The Amoeba seen creeping in the form of an extended club towards the source of nourishment affords an answer to the question of how it is possible to have permanent shape of the organism where there is active movement of its particles. Given unchanging outward conditions, the form depends wholly on the unchanging character and direction of the metabolism. In a fountain or a gas jet, although the particles are in constant movement, not one of them retaining the same position for a moment, the entire jet retains its characteristic form as long as it is subject to the same conditions. The same is the case with living matter. A cell, in spite of its active metabolism, appears to us to be in repose. It gives us the impression of immovability, just as a gas or water jet conveys that impression although each particle is in rapid and incessant movement.

This view of the relation between metabolism and form gains an additional interest when applied to the phenomena of development. It is evident that if the metabolism of a cell is continually changing, the changes will find expression in the form of the organism, so long as this is not prevented by factors operating outside the organism. In this way, development is brought about. We know that the metabolism of the egg cell is from the first continually changing. The supplies of reserve nourishment are consumed and other matter appears in the cell and in its descendants. Here we have a marked example of the close connection between metabolism and change of form.

In this connection I would protest against the very wide-spread opinion that the egg cell, especially in the higher animals, must have a highly complicated molecular structure, much more complicated than that of any other cell. This appears to me to be an absolutely groundless assumption, recalling the so-called "Einschachtelung Theorie". Because a highly complicated organism develops from the microscopical egg cell, it is thought that the molecular structure of the latter must be highly complicated. I do not doubt that it is complicated, but I deny the assumption

that it is more complicated than the molecular structure of any other cell. We have only to imagine that the metabolism in the egg cell is continually changing, never remaining the same for two consecutive moments, so that each condition causes the following condition and is itself the outcome of the condition last preceding it. Considering how close is the connection between metabolism and change of form, each change in the metabolic exigencies of the developing organism must be responded to by a further and more complicated structural change. The assumption of greater complication of the molecular structure of the original egg cell is thus entirely superfluous.

It may appear as if the idea of molecular structure of living substance is inconsistent with that of the continual flow of matter. We have here, however, on a small scale, the same relation as that existing between change of form in the organism, and metabolism. Metabolism consists in chemical processes. These processes, however, are only brought about because each atom or group of atoms or molecules attracts, by chemical affinity, other atoms, group of atoms or molecules in a certain direction. This causes a continual flow of matter, some atoms or groups of atoms being withdrawn and others taking their places. If these atoms and groups of atoms are always of the same kind, and if their entrance and exit always take place in the same manner and direction, as must be the case so long as the metabolism of the whole remains unaltered, a certain ordering of the particles results which we must call structure although the whole substance is in motion, in a continual flow. It is only in this way that, for instance, the phenomena of the regeneration of the cell can be explained. A cell from which a portion has been removed can regain its original form provided that it is capable of producing the reserve matter required for its reconstruction. The reserve matter will reach the injured part through the usual channels, being attracted thither by the remaining particles, etc. Should the injured cell no longer have the power to produce the necessary matter for regeneration, *i.e.*, if the entire metabolism has suffered lasting injury, the recon-

struction of the lost part is impossible. If an Infusorian cell, for example, of a very characteristic and complicated form is cut in such a manner that only the one half retains the nucleus, all the cell particles requisite to life are to be found in this half, and these, through metabolism, will soon reproduce the original shape of the cell. The metabolism of the other half, on the contrary, having been permanently injured, it will slowly die, being incapable of regeneration. This important fact has been proved by a great number of experiments made by Nussbaum, Grüber, Balbiani, and others.

We thus find metabolism to exist in the closest causal relation with the production and preservation of form, and in all investigations and experiments on the mechanism of form-evolution it must not be lost sight of as constituting an important factor.

MAX VERWORN.